The fate of non-selected activity in saccadic decisions: distinct goal-related and history-related modulation.

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ABBREVIATED TITLE:

The fate of non-selected activity

1 ABSTRACT

The Global Effect (GE) traditionally refers to the tendency of effectors (e.g. hand, eyes) to first land in between two nearby stimuli – forming a unimodal distribution. By measuring a shift of this distribution, recent studies used the GE to assess the presence of decision-related inputs on the motor map for eye movements. However, this method cannot distinguish whether one stimulus is inhibited or the other is facilitated and could not detect situations where both stimuli are inhibited or facilitated.

Here, we detect deviations in the bimodal distribution of landing positions for remote stimuli, and find that this bimodal GE reveals the presence, location and polarity (facilitation or inhibition) of history-related and goal-related modulation of the non-selected activity (e.g. the distractor activity in correct trials, and the target activity in error trials). We tested, for different inter-stimulus distances, the effect of the rarity of double-stimulus trials, and the difference between performing a discrimination task compared to free choice.

Our work shows that the effect of rarity is symmetric and decreases with inter-stimulus distances, while the effect of goal-directed discrimination is asymmetric – occurring only when the distractor is selected for the saccade – and maintained across inter-stimulus distances. These results suggest that the former effect changes the response property of the motor map, while the latter specifically facilitates the target location.

2 NEW & NOTEWORTHY:

Deviations in landing positions for saccades to targets and distractors reveal the presence, location and polarity of history-related or goal-related signals.

Goal-directed discrimination appears to facilitate the target location, rather than inhibiting the distractor location,

Rare occurrence of a choice appears to indiscriminately increase the neural response for both locations.

3 INTRODUCTION

No matter how efficient a decision-making system, its expression will ultimately be limited by the mechanisms used to translate decisions into actions. Those mechanisms can be seen as an encryption key to decipher decision-related signals from motor responses (e.g. eye or hand movement trajectories). In the context of saccadic eye movements, the Superior Colliculus (SC) is a key motor interface (a role shared with the Frontal Eye Field), integrating several sources of input to produce motor signals guiding the eye trajectories (for eye trajectories and SC activity, see, for instance, Goossens & van Opstal, 2012; White & Munoz, 2011 for a review on SC).

To model the saccadic motor interface it is common to use a race-to-threshold mechanism allied with a winner-take-all policy (Kopecz 1995; Kopecz and Schöner 1995; Trappenberg et al. 2001; Bompas and Sumner 2011, 2015, Satel et al. 2011, 2014; Wang et al. 2011; Marino et al. 2012). In these models, the race-winner both triggers (in time) and selects the destination for the next saccade; 'when' and 'where' are tightly coupled. Although these modelling efforts help us deduce the temporal dynamics of decision-related signals, they have not focused on the details of spatial selection (Wang et al. 2012a). In short, these models are optimized to explain only one side of the coin.

In other models the 'where' and 'when' processes are more loosely coupled (Findlay and Walker 1999; Arai and Keller 2004; Wilimzig et al. 2006). This low coupling is twofold: 1) the 'where' processes are not necessarily completed when the 'when' processes trigger a saccade; 2) all the activity present on the motor map is taken into account to generate the 'where to move' motor response (except in Findlay & Walker, 1999). The first idea can be illustrated with the saccadic curvature literature, where the incomplete interplay between target and distractor signals changes with saccade latency to produce curvature either towards or away from the distractor (McPeek et al. 2003; McSorley 2006). The second point was demonstrated by observing the SC/FEF activity during saccade curvature (McPeek et al. 2003; McPeek 2006) or by reconstructing saccade trajectories from activity recorded in the SC (Goossens and Van Opstal 2006). Finally, the low coupling between 'when' and 'where' is in line with recent results suggesting there is no winner-take-all in the SC motor interface in mice (Phongphanphanee et al. 2014). The rationale, then, is that using a model of spatial interactions with a low coupling between 'where' and 'when' as a decryption key, saccade metrics can be used to characterize specific decision-related signals projecting onto the SC.

When two close visual stimuli are presented simultaneously, eye movements directed to one of them tend to land in between the two stimuli, betraying a spatial interaction (Findlay 1982; the Global

Effect, Deubel et al. 1984; see also Sailer et al. 2002 for hand movements), illustrated in Figure 1E,F. This Global Effect (GE) has been the topic of intensive investigation in the eye movement community to understand how visual stimuli interact in, or upstream of, the saccadic motor interface (Casteau and Vitu 2012; Tandonnet et al. 2012; Tandonnet and Vitu 2013; Van der Stigchel and Nijboer 2013). Two main accounts for the GE have been suggested (reviewed in the discussion of Katnani and Gandhi 2011) and they mainly differ in the order of their operations: the averaging mechanism and the transformation from SC space to visual/saccadic space.

The first account, which is compatible with winner-take-all models, assumes a merging mechanism driven by a specific pattern of lateral interactions in the SC (short range excitation, long range inhibition). Regions of activity induced by two *close* stimuli would merge into a single zone of activity located between them, as illustrated in Figure 1A/E (Arai et al. 1994; Kopecz and Schöner 1995; Wilimzig et al. 2006). To apply a winner-take-all in this case is equivalent to taking the average position between stimuli in SC space and then project the result to saccadic/visual space. Thus the landing positions of saccades would form a straight line in SC space, and an outward C-curve in the visual space (for a more detailed explanation, see Katnani and Gandhi 2011).

The second account suggests that vector averaging occurs when the population activity of the SC is decoded into a command for the extra-ocular muscles. Regions of activity of any two stimulations would *not* merge; the mechanism downstream would simply program the saccade corresponding to the average of all the saccadic vectors activated in the SC (Lee et al. 1988; Goossens and Van Opstal 2005; Van Opstal and Goossens 2008; Gandhi and Katnani 2011; Katnani et al. 2012), as illustrated in Figure 1B/F. Note that this vector averaging mechanism has also been used to explain trajectory curvatures in hand and eye movements (Tipper et al. 1997; McSorley et al. 2004; Walton et al. 2005). Here, the averaging is applied directly on the saccadic vectors, which means that the average happens in visual/saccadic space. Thus the landing positions of the saccades would form a straight line in visual space and an inward C-curve in SC space(for a more detailed explanation, see Katnani and Gandhi 2011).

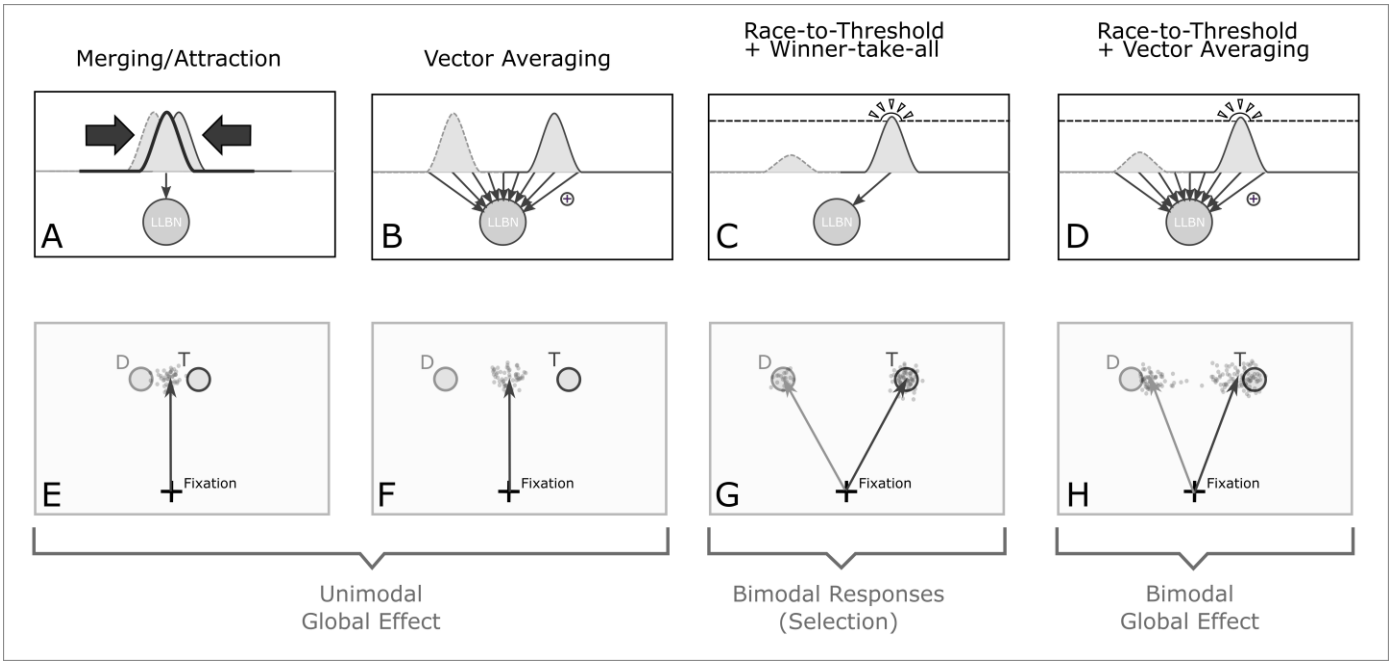


Figure 1:Schematic of different mechanisms that could be involved in the spatial decision process. On the top row*, we represent different mechanisms that have been proposed for the saccadic motor map or downstream machinery. The dark-edged and bright-edged curves stand for the activity of the target and distractor, respectively. The horizontal dashed line represents a hypothetical saccade initiation threshold.* ***On the bottom row,*** *we represent the effect of those mechanisms on saccade direction. The arrows represented the average saccadic vector for each distribution mode while the dots draw the distribution of the saccade endpoints. The bright-edged and dark-edged disks represent, respectively the distractor and the target on the monitor screen. The black cross is the fixation stimulus.* ***Panel A/E*** *present the merging mechanism proposed to explain the unimodal Global Effect. We highlight that this mechanism works on stimuli that are close enough for their activity to overlap.* ***Panel B/F*** *show the vector averaging mechanism – where the overall activity on the motor map is integrated by the Long Lead Burst Neurons (LLBN, dark-edged disk) – that has also been suggested to explain the unimodal Global Effect. We highlight that it would work on remote stimuli.* ***Panel C/G*** *represent a race-to-threshold mechanism that triggers and generates the saccade corresponding to the first point of activity to reach the threshold on the motor map. In* ***Panel D/H*** *we suggest that a combination of the race-to-threshold mechanism (****C****) and vector averaging (****B****) would lead to a bimodal Global Effect (see text for more details).*

When two simultaneous visual stimuli are remote rather than close, the landing position of the saccades tends to form a bimodal distribution. Such bimodal distribution can be explained by a race-to-threshold model combined with a winner-take-all mechanism (**Figure 1**C/G). In such a model, the first zone to reach threshold would simply trigger an eye movement to the corresponding stimulus, as illustrated in Figure 1C. As this system only retains the race winner, this would mean saccades are directed either to one stimulus or the other; in such models the losing stimulus could affect the latency (e.g. via lateral inhibition) but not the final destination of the action (Figure 1G).

However, while the GE traditionally refers to circumstances in which a unimodal distribution of landing positions is observed between two relatively close stimuli ("genuine global effect", Van der

Stigchel and Nijboer 2013), there are indications that spatial interactions continue to occur for bimodal distributions when stimuli are further apart (Arai et al. 2004; Van der Stigchel et al. 2011). More evidence can be found in the saccade curvature literature in which a correlation between the initial directions and the landing positions of the saccades was reported (Van der Stigchel et al. 2007) for inter-stimulus distances that do not evoke unimodal GE. Based on this evidence, it seems that, even when saccades appear to be successfully directed to one stimulus or another, and do not land half way in between, close examination of the endpoints reveals some attraction or repulsion to/from the other stimulus (Figure 1H). This phenomenon, which we will refer to as the bimodal GE, could be explained neither by a merging nor by a vector averaging mechanism taken alone. The first aim of our article is to confirm and characterize the bimodal GE, and propose a simple model that can account for it.

This 'bimodal GE' could be explained by a model that features a low coupling between 'when' and 'where' to move. It would combine a race-to-threshold mechanism, which triggers the saccade, with a vector averaging mechanism specifying the spatial destination (**Figure 1**D). Such a model is similar to that of Arai and Keller (2004) or Wilimzig et al. (2006). It would have to feature relatively low mutual inhibition so that the race loser maintains some activity at saccade onset (such as in McPeek et al. 2003) to influence the saccade metrics through the vector averaging (Figure 1D, and such as in Goossens and Van Opstal 2005; Van Opstal and Goossens 2008), predicting small deviations of the endpoints towards the losing stimulus (Figure 1H). This simple model predicts that such deviations ought to lie on a straight line in visual space and an inward curve in SC space, given that they are not occurring through merging within the SC.

If the bimodal GE is robust and our logic holds that it reflects residual activity for the *loser* in an incomplete decision process, then systematic modulation in bimodal GE should reflect the strength of this losing activity. This activity should change over time, being stronger at earlier points in the decision process. It has often been suggested that the relative importance of non-specific signals and discriminatory signals changes with latency, such that early inaccurate responses are relatively more driven by non-specific transient visual responses in the SC/FEF drive, while later more accurate responses are more driven by slower signals carrying more task-relevant information (Bompas and Sumner 2011, 2015; see also Boehnke and Munoz 2008; Schall et al. 2011). Heeman et al. (2014) found this relationship in the unimodal GE in a discrimination task: smaller GE was associated with longer latency. Our conceptual model for the bimodal GE predicts this same relationship: larger GE should be associated with shorter latency when the decision process is least complete.

Once we establish that the bimodal GE is systematically modulated in a way consistent with changing activity for the losing action option, it becomes a means to test aspects of theory that could not be tested with the unimodal GE, such as whether distractors are inhibited or targets facilitated during target selection. This can be achieved in a straightforward paradigm where the participant starts a trial by fixating a fixation cross and is instructed to make a saccade to peripheral stimuli as soon as they are presented. Single stimulus trials, in which only one peripheral stimulus is presented, are interleaved with double stimulus trials, in which two peripheral stimuli are presented. In the latter condition, the participant faces a choice situation (section 4.3 describes our paradigm in more detail). The type and context of the double stimulus trials can then be manipulated to assess how endpoint deviations at distractor and target locations are affected differently by endogenous signals.

Two types of endogenous signals can be fundamentally distinguished: goal-related and history-related (Awh et al. 2012). In the traditional GE paradigm, goal-related signals have been probed by comparing a discrimination task to a free choice condition – i.e. whether one stimulus is designated a target, or saccades to either stimulus are allowed. Although early studies failed to demonstrate goal-related effects (Ottes et al. 1985), more recent evidence clearly shows it (Heeman et al. 2014) while some clinical studies used it to probe the role of FEF in shaping the target discrimination signal (Van der Stigchel et al. 2013). Note that Heeman et al. (2014)'s results were predicted by the aforementioned model of Wilimzig et al. (2006), which features a low coupling between 'where' and 'when' to move. However, the unimodal GE could not distinguish whether goal-related signals enhance the target or inhibit the distractor. This is also difficult to distinguish in term of latencies, where global slowing due to mutual inhibition, slower perceptual discrimination or increased caution could mask or interact with any facilitation or inhibition effects on target and distractor individually. With the bimodal GE, the distinction should be clearer: target enhancement would manifest as increased GE for saccades to the distractor (i.e. when the target *loses* the race), while inhibiting the distractor would diminish GE on saccades to the target (when the distractor loses the race; see **Figure 2**).

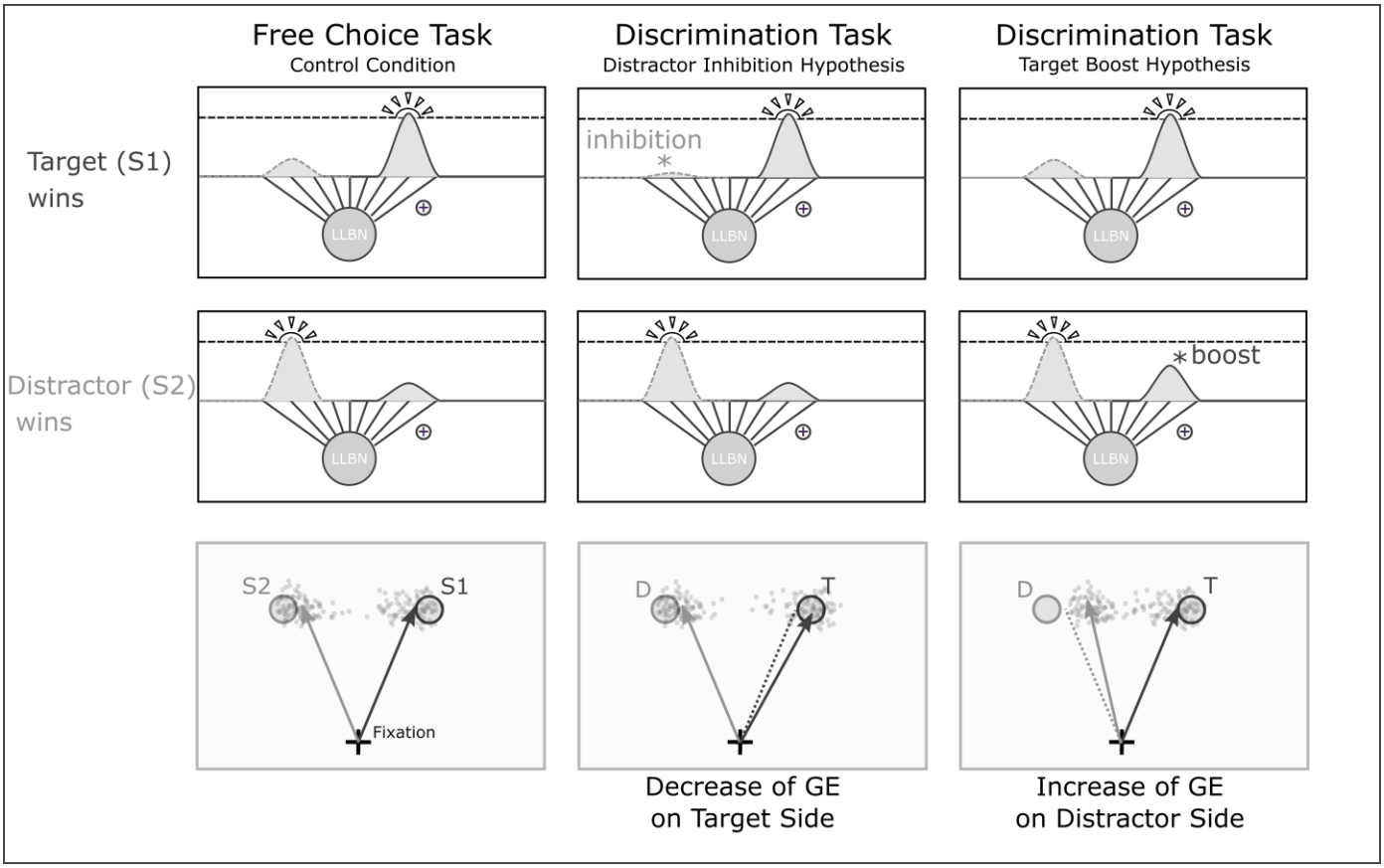


Figure 2: Hypotheses for the Effect of Discrimination Task. *Rows 1 and 2 depict the activity for the target and the distractor (dark and bright curves, respectively) on the motor map when one of them reaches the threshold to trigger a saccade. Row 3 shows the predicted distributions of saccade endpoints. The participant is presented with a pair of similar stimuli and is either required to make a saccade to the target and ignore the distractor (discrimination condition), or is able to freely select one of them to make a saccade (free choice condition; for consistency, we call one stimulus the target and one the distractor in all conditions). In free choice (Column 1), we expect the bimodal Global Effect will be similar on S1 and S2 side, since the participant should treat them as equivalent (Row 1). In the discrimination task, we expect the target stimulus to be relatively advantaged, and thus the pattern may not be symmetrical. Under the assumption that the distractor is inhibited while the discrimination progresses (Column 2), the activity of a loser distractor (Row 1) would be less than that of a loser target (Row 2), leading to less bimodal GE on Target side – as compared with free choice (Row 3, dark dashed line). Under the assumption that the target is boosted (Column 3), we would predict an opposite pattern (Row 1 & 2), and the bimodal GE on the Distractor side would be larger compared to free choice (Row 3, bright dashed line).*

History-related signals, such as the spatial probability of the target, are also known to affect the GE (He and Kowler 1989; Wang et al. 2012b). However, history-related signals that are spatially nonspecific –such as the probability of occurrence of double-stimulus trials – would affect equally both stimuli and could not be detected with the unimodal GE. Thus, their effect is unknown. When comparing a condition with rare double-stimulus trials to a condition with frequent double-stimulus trials, we hypothesized that rarity of double-stimulus trials could make both stimuli more salient,

leading to an increase of the bimodal GE for saccades to both stimuli (see **Figure 3**). Alternative hypotheses would be no effect for spatially non-specific history, or an enhancement for frequent conditions as occurs for spatially specific history effects.

Finally, because the bimodal GE can be measured over a large range of inter-stimulus distances, we expect that it can be used to assess the spatial properties of the above signals. Specifically, we aimed to investigate whether the effect of probability (or relative surprise) is similar to goal-related signals (and at the same time, we explore which distance is best to study the bimodal GE).

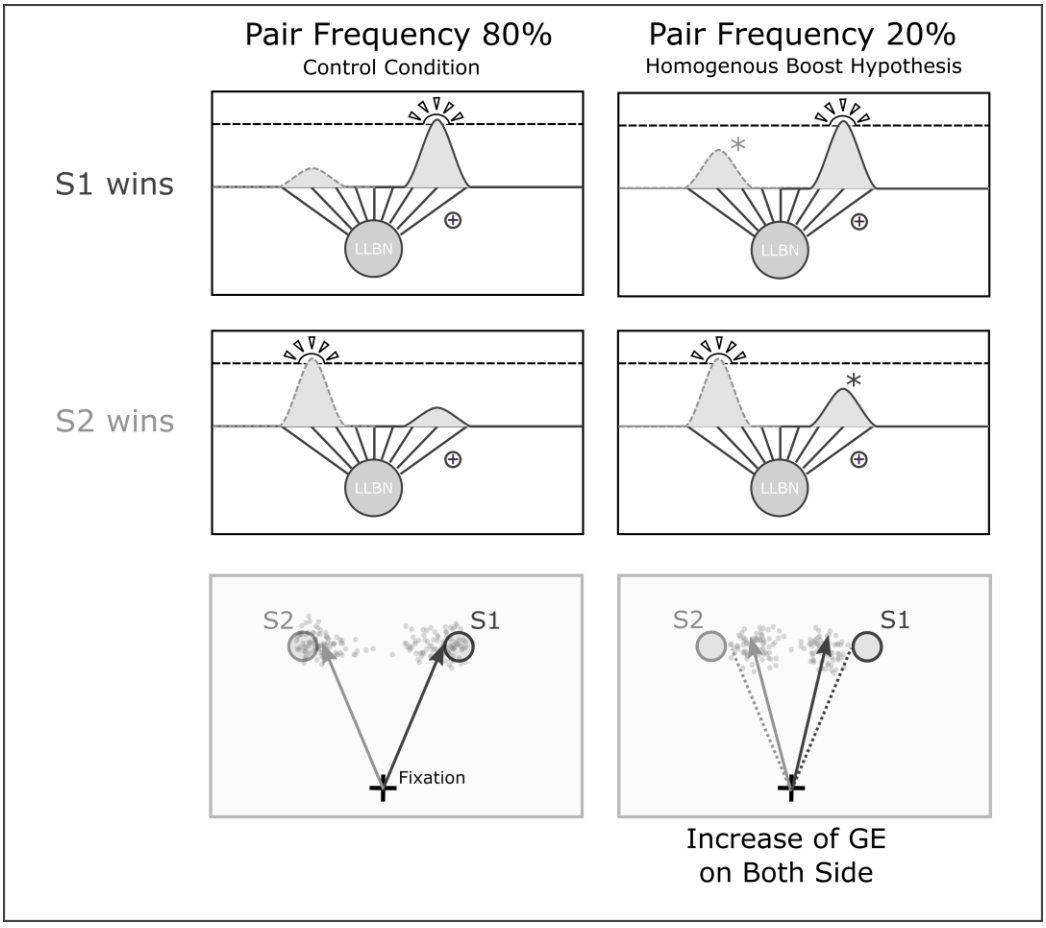


Figure 3: Hypothesis for the effect of Rarity. *Row 1 and 2 depict the stimulus-related activity on the motor map when one of the stimuli (S1 and S2, respectively in dark and bright gray contours) wins the race-to-threshold to trigger a saccade. Row 3 presents the predicted distributions of saccade landing positions. We hypothesized that there could be a homogenous boost of the signals reaching the motor map when the context is unfamiliar (a surprise effect). In the control condition (Column 1, Pair Frequency 80%), the pair of stimuli is presented only for 80% of the trials while in the test condition (Column 2, Pair Frequency 20%), the pair of stimuli is presented only for 20% of the trials. Under the above assumption, we predict that the activity of any race looser (S1 or S2, first and second row) should be greater in Pair Frequency 20% than in Pair Frequency 80%. Thus the bimodal Global Effect would be larger on both stimulus side (third row) when compared to control.*

4 METHODOLOGY

4.1 PARTICIPANTS

Four naive individuals and the author (25-27 years old; 3 males and 2 females) participated in the experiment. All had normal visual acuity, were postgraduate at Cardiff University, had given their written informed consent and received payment for their time. No participants reported drug or alcohol dependencies or sleeping disorders. Ethical approval was obtained through the local ethics committee. All but one were naïve to the purpose of the experiment

4.2 APPARATUS

Participants performed the experiment in a quiet dark room. They sat at a distance of 72 cm from a CRT monitor (ViewSonic P225f) with a 100 Hz refresh rate. Its dimensions were 36.60 cm in width and 29.30 cm in height for a density of pixels approximately 35 PPCM (pixels per centimeter). The monitor was covered with a red filter. Eye movements were recorded with an Eyelink 2000 system (Tower mount system; SR Research Ltd., Canada), an infra-red video-based eye tracker that has a spatial resolution of 0.01° and a typical average accuracy between 0.25° and 0.5°. It was used at a time resolution of 1000 Hz while the participant's chin was resting on the headset pad. Only the left eye was recorded. The experiment was programmed with *pygame*, a python library that provides graphic and input management, and *pylink*, the official Eyelink library for python. All the analyses were conducted with scipy (McKinney 2010), the scientific package for python (e.g. www.python.org), and with ipython 2.0 (Perez and Granger 2007). The source code and data are available on the open science framework (*https://osf.io/9adbk/*).

4.3 STIMULI AND PROCEDURE

All the trials followed the same template: the participant started by staring at a white fixation cross of radius 0.4° (luminance: 4.5 cd/m^2 except when stated otherwise) on a black background at the center of the screen. After a random interval of 500-1000ms, the fixation cross disappeared and a target element was presented at an eccentricity of 13.5° (see **Figure 4**A and B) while its direction could have been any one of the 32 directions tested. We tested 8 directions per quadrant (given in directional angles, see **Figure 4**A): from +5.625° to +45° by steps of 5.625° for the top right quadrant; and reciprocally for the other quadrants (see Figure 4A). For a certain percentage of the trials (double

stimulus trials), an additional stimulus is simultaneously displayed at the horizontal mirror image of the target: if the target is presented in the top part of the screen (e.g. at 45°), the additional stimuli will be displayed symmetrically in the bottom part of the screen (e.g. at -45°). The stimuli remained present until after the end of the saccades analyzed here. Following this, the screen was cleared and a new trial began.

We tested the effect of the task performed by the participants when a pair of stimuli was presented (Task-Type). In Free Choice Task conditions (Free Choice), the additional stimulus was identical to the target but 12.5% brighter. For these conditions, the participants were simply asked to move their eye to any presented stimulus as quickly and precisely as possible. They did not receive further instructions for the case of double-stimulus trials. In the Discrimination Task (Discrimination), the additional stimulus was of a different shape to the target and was also 12.5% brighter. For these conditions, the participants were instructed to ignore the distractor and to move their eyes to the target as quickly and precisely as possible. For different blocks, the distractor and the target of *Discrimination* conditions could either be a circle or a diagonal-cross of 0.8°. The distractor logically inherited the remaining shape: it was a circle if the target was a diagonal-cross and vice versa.

We tested the effect of frequency of occurrence of the pair of stimuli: in High Frequency conditions (F-80), the additional stimulus was presented 80% of the time, while, in Low Frequency conditions (F-20), its frequency was set up at 20%.

One experimental session would test one of the 4 following combinations: *F-20/Free Choice*, *F-20/Discrimination*, *F-80/Free Choice*, *F-80/Discrimination*. For all the participants, the sessions were ordered as follows: *F-20/Free Choice*, *F-20/Discrimination*, *F-80/Free Choice*, *F-80/Discrimination*, *F-80/Discrimination*, *F-80/Free Choice*, *F-20/Discrimination, F-20/Free Choice*. While we would usually counterbalance the order across participants, here we thought it was useful to keep this order since surprise in F-20 conditions is part of the design rationale and participants were not told whether there will be double-stimulus trials. The palindrome order within participant was used to minimize any linear training effects. We also check that our results hold when order effects are taken into account.

The participants were required to undertake 8 sessions of 1600 trials each (8x60min); each session being separated at least by one night. A break was offered every 200 trials while a break and a calibration on 13 points were imposed at every 400 trials.

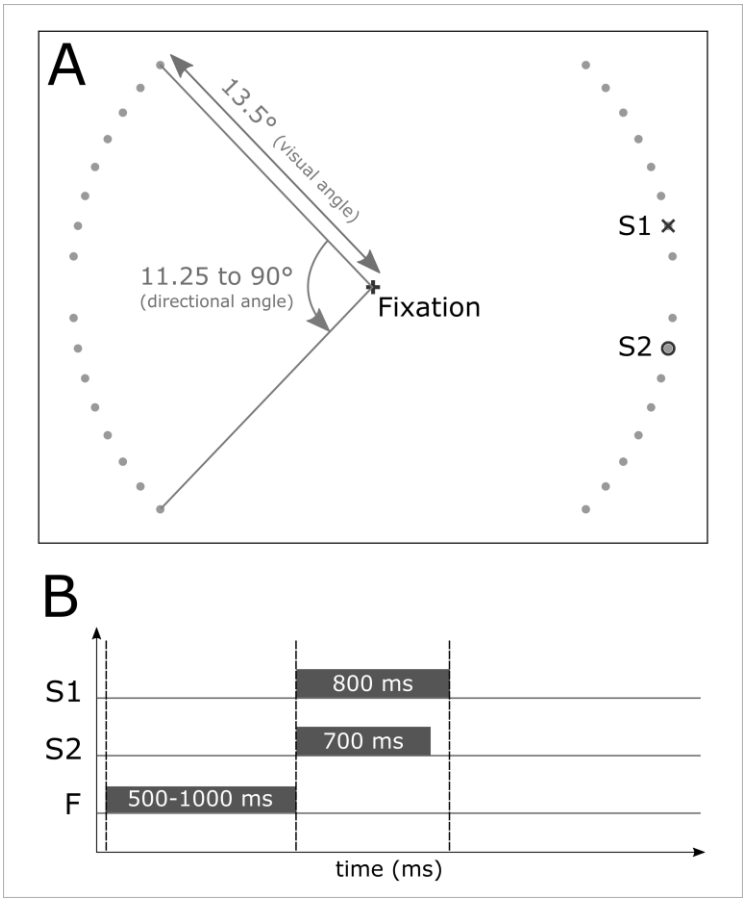


Figure 4: Summary of the Paradigm. A: *the possible positions of the stimulus on the monitor's display during a trial (light gray dots); the eccentricity of the stimuli was always of 13.5° while their directional angles varied from 5.625 to 45° (by step of 5.625). The stimulus pair in double-stimulus trials was always symmetrical that one stimulus was presented in the upper hemi-field and the other in the lower hemi-field (same eccentricity, opposite directional angles). The schematic illustrates a Discrimination Task trial where the S1(in dark gray) is a diagonal-cross and the additional stimulus S2 (in dark gray) is a circle. Note that the color of the background and stimuli are not respected in this schematic, and the array of possible stimulus locations (light grey dots) was not visible to the participant.* ***B:*** *A pair of stimuli –S1 and S2- appeared on the screen simultaneously after the offset of the fixation cross F.*

4.4 Data Analysis

4.4.1 Saccade Detection and Cleaning

Saccade end points were detected as the first data point with a velocity below $10°.s^{-1}$, an acceleration below $6000°.s^{-2}$, and a shift from the previous fixation above 1.0°. Thensaccade start points were detected as the last data point (backward from the saccade end point) at which the eyes had a velocity below $30°.s^{-1}$, an acceleration below $6000°.s^{-2}$, and a shift from previous fixation below 0.3°. The difference in criteria for saccade end and start points were implemented to deal with an artifact that

can occur at the end of saccades (see (Nyström et al. 2013), for more information of this post-saccadic oscillation artifact). Trials were automatically marked as suspect and inspected if: 1) there were missing values or gaze positions outside the monitor during the saccade, 2) no entire saccade was detected, 3) the reaction time from target onset was less than 80ms, 4) the saccade duration was longer than the reaction time, and 5) the position shift from the fixation was less than 7.5°. In addition, the experimenter could allow some trials that presented a position outside the monitor display, or reject a trial that presented a blink. After cleaning, the loss rates were 1.7%, 1.5%, 4.5%, 3.4% and 2.2% (given for each of the 5 participants). Note that we included all the saccades made toward Target and Distractor side in the Discrimination task. We also included all the saccades toward S1 and S2 in the Free Choice task.

4.4.2 Measure of the Global Effect: Distance From the Closest Attractor

The landing positions correspond to the endpoint positions of the first saccade produced after the onset of the stimuli. Note that for each of the 8 stimulus distances that we tested, there were 4 possible target positions (one per quadrant); for the analysis, the data were mirrored and combined across these.

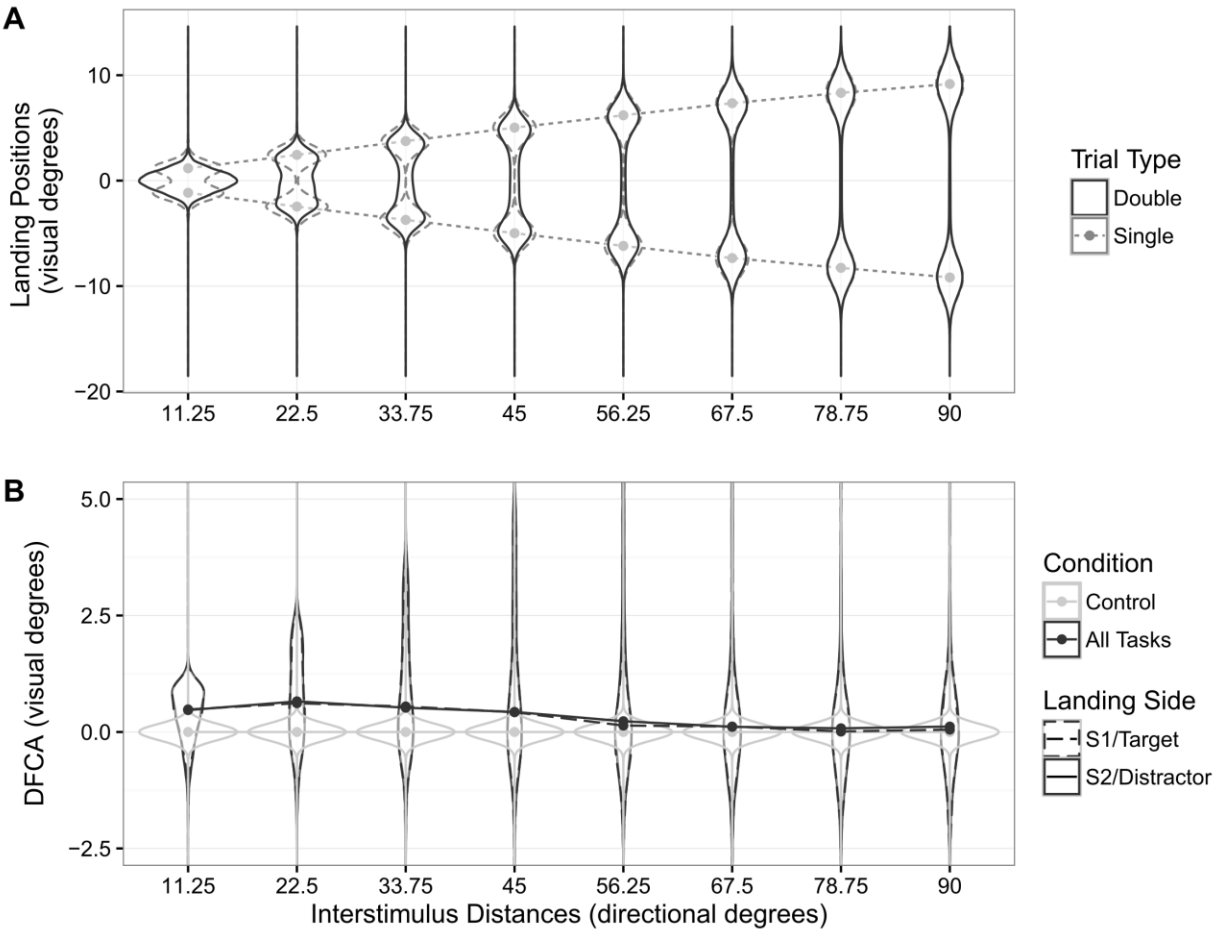


Figure 5: Landing Positions and Distance From the Closest Attractor. *We used violin plots to present the data distributions – the larger the violin, the denser the data points at that y-position. For instance,* ***in A****, the dark violin for the inter-stimulus distance 11.25 shows a unimodal distribution of landing positions centered on 0 – that is exactly between the two stimuli. The brighter violin is the control distribution from single-stimulus trials with the same locations. The dashed lines are the means of the control modes. While the inter-stimulus distance increases, the distribution splits progressively into a bimodal distribution that is eventually indistinguishable from control.* ***In B****, we plot the distance from closest attractor (DFCA), so that the transformation can be observed by comparing the top plot and the bottom plot (see section 4.4.2 for further details). The DFCA on each side is simply the landing positions in double-stimulus trials centered on the mean of the landing positions in single-stimulus trials. The lines with dots represent the means of the distributions. The data are from all the participants and all conditions.*

To measure the bimodal GE, we divided the landing positions into two groups one directed towards the target, and another directed towards the distractor. For each group, we computed a control landing position from the single-stimulus trials. We then examined the deviation of each group from their control. The controls were computed across the four screen quadrants (we mirrored the data and collapsed them to one quadrant), and are distance specific (e.g. one control per distance), participant specific, and block specific (to correct for calibration discrepancies). We named the

measure the Distance From the Closest Attractor (DFCA) – the attractors being the control positions. For the landing position *i* and on the y-axis, this is defined mathematically, by:

$$DFCA_i = \min(|C_1 - y_i|, |C_2 - y_i|)$$

Where C1 and C2 are the control position. **Figure 5** shows the DFCA for saccades directed toward the target. Note that another major difference with the usual measure of the GE is that we get one measure per trial, which increases the statistical power.

4.4.3 Statistical analysis

To test statistically the difference in DFCA across conditions and distances, the saccades of all the participants were gathered (as in Van der Stigchel & Nijboer, 2013). This led to an average of 389 trials for each distance in each condition for the conditions *Free Choice* | *F-20* and *Discrimination* | *F-20* and an average of 1,543 trials for conditions *Free Choice* | *F-80* and *Discrimination* | *F-80*. The proportion of landing positions between the two stimuli was reasonably balanced in all conditions and participants. Given that the distributions of DFCA are clearly non-normal and have different shapes across distances, we used the non-parametric independent 2-group Mann-Whitney U-test to test for mean differences (the `wilcox.test(x, y, paired=FALSE)` in R). In order to focus on differences within participants, and because the U-test does not apply this by itself, we applied a within-subject correction (Cousineau 2005) by centering the data of each participant on the same mean.

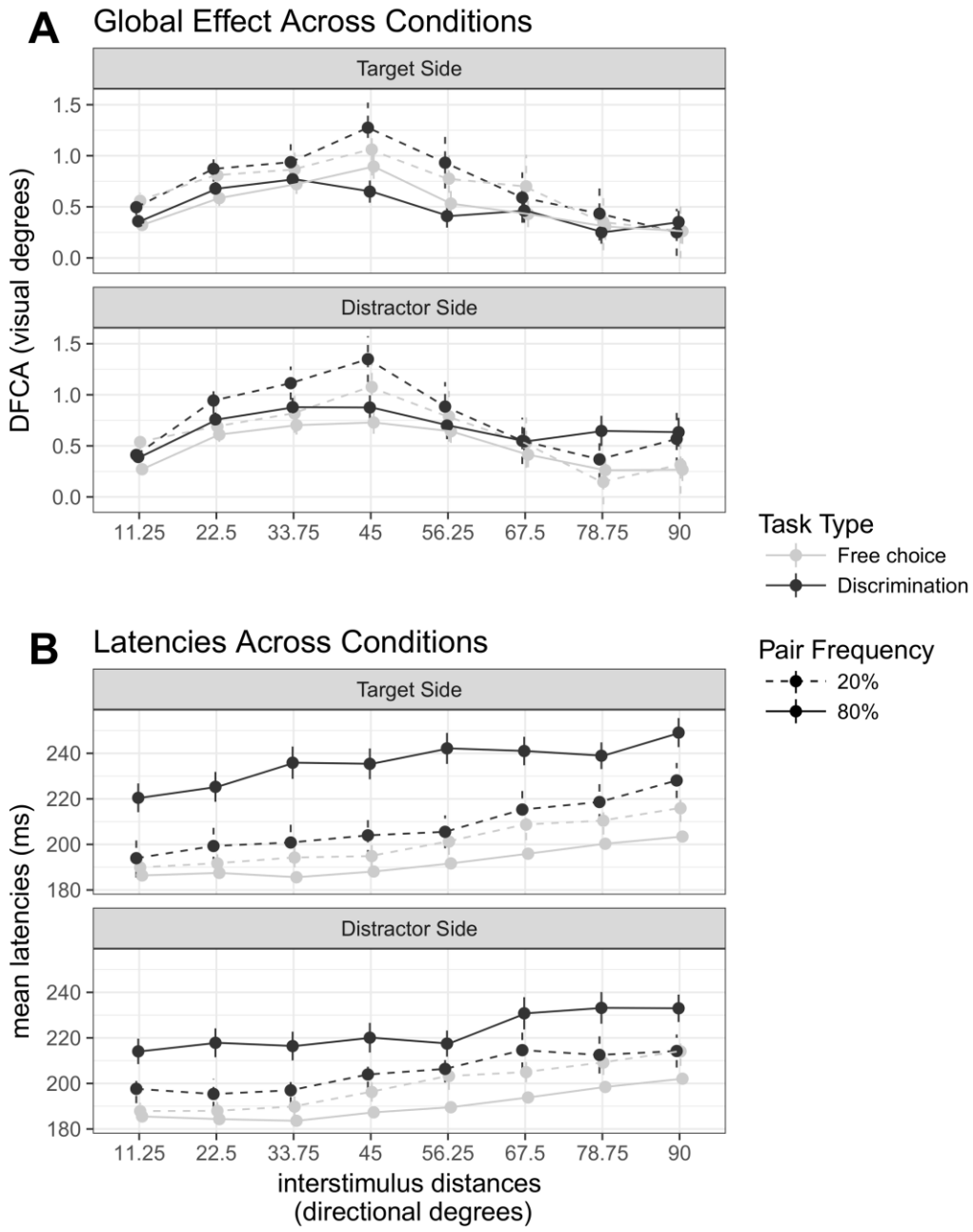
Using the DFCA, we ran one U-test for each of the eight stimuli distances testing for an effect of *Task-Type* (*Discrimination* against *FreeChoice*). The same procedure was repeated to test the effect of *Pair-Frequency* across stimuli distances (level *F-20* against level *F-80*). The p-values for a set of tests were corrected according to Hommel's correction, which has been recommended for adjusting mildly correlated p-values (Blakesley et al. 2009). We report, in Figure 7, the Hodges–Lehmann estimator (HLΔ) – i.e., the median of pairwise differences in bimodal GE between two conditions. This can be interpreted as the GE modulation between the two tested conditions. A complete report of the U-test statistic can be found on the OSF repository.

5 RESULTS: DISTANCE FROM CLOSEST ATTRACTOR

5.1 OVERVIEW OF THE BIMODAL GE

Observation of **Figure 6**A reveals a clear bimodal GE effect, and that the DFCA initially increases and then decreases with stimulus distance (one-way ANOVA, $F(7, 28)=2.9$, $p = .02$, $\eta_g^2=.42$), which is how the GE was expected to fluctuate. **Figure 6**B reveals that latencies increase with stimulus distance in all conditions (one-way ANOVA, $F(7,28)=9.9$, $p<.001$, $\eta_g^2=.712$); this could, at least partially, explain the aforementioned decrease of bimodal GE. Note that this tendency is also present in FreeChoice, where there is no discrimination to perform. Thus, lesser Global Effect with longer latency could be interpreted as a stronger commitment to one stimulus with time.

Figure 7 shows landing positions of a representative participant both in visual and SC space. The landing positions are distributed along a straight line (slightly curved inward) in visual space and along a C-curve when projected in an approximation of the human SC space (based on the monkey data in Robinson 1972; according to Ottes et al. 1986 's equations). As discussed in Introduction, this pattern is what we would expect from a saccadic vector averaging mechanism; and it echoes back to the pattern obtained when applying simultaneous, weighted supra-threshold micro-stimulations to the SC (Katnani and Gandhi 2011; Katnani et al. 2012).



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389 ***Figure 6: Overview of the Distance From the Closest Attractor (DFCA) and Latencies over stimuli***
390 ***distances and between conditions.*** *The figure shows the mean of the distributions with the parametric 95%*
391 *confidence intervals; the top part displays the curves for the DFCA on the target side, and the bottom part*
392 *displays the curves for the DFCA on the distractor side.*

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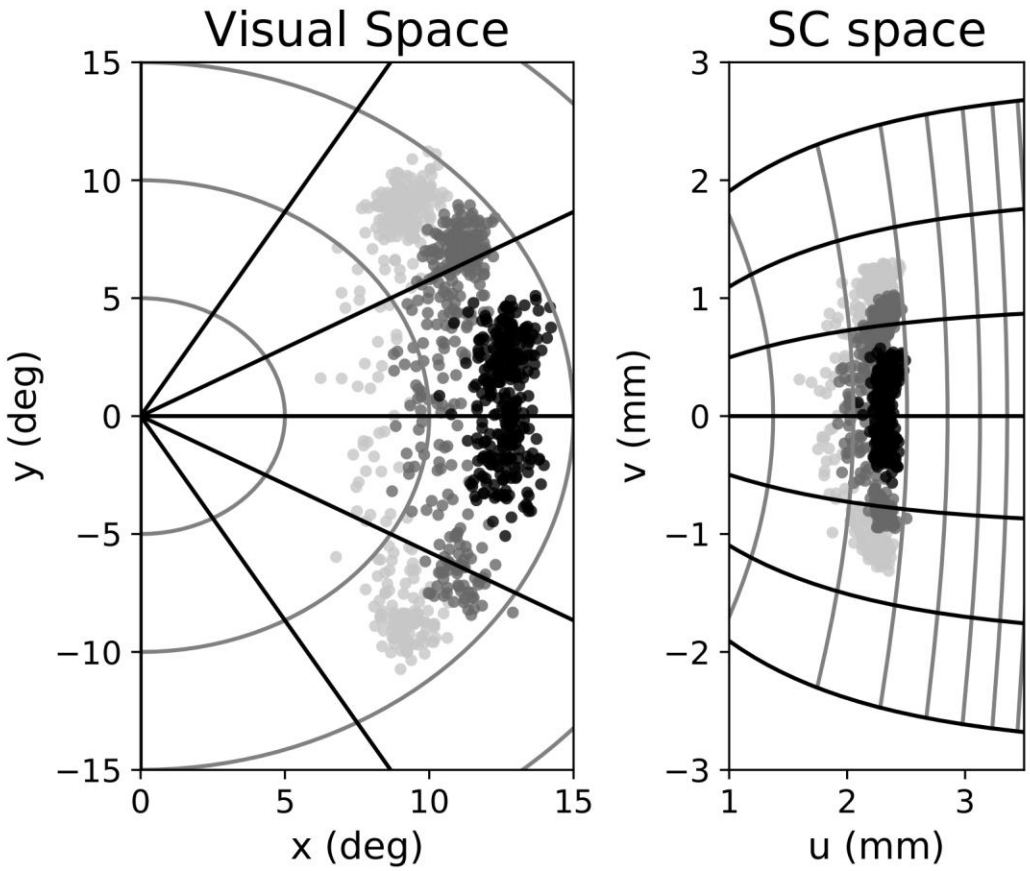


Figure 7: Distribution of Landing Positions in visual space and Superior Colliculus (SC) space from a representative participant. *Distributions are shown for inter-stimulus distances 90° (light grey dots), 67.5° (medium gray dots) and 33.75° (dark gray dots) in F80/Discrimination Task. The distributions followed an inwards C-curve on the SC space; this was a consistent pattern across conditions and participants (the figures for all participants are accessible on the OSF repository). The landing position were projected to an approximation of the human SC space; using Ottes et al.(1986)'s equations and its original set of parameters that estimates the electrical stimulation data from Robinson (1972) on monkey.*

As noted in introduction, it is important to establish that the bimodal GE is modulated in size in a systematic way consistent with representing the losing activity in an incomplete decision process. We expect that saccades landing in between the two stimuli would have the shorter latencies, driven by early nonspecific visual transients that are equivalent for both stimuli. Smaller deviations and accurate saccades (to either the target or distractor) would be associated with longer latency when the decision process has progressed towards a unique winner (i.e. the losing activity has diminished). Figure 10 shows that these predictions are confirmed in our data, consistently for every condition and every distance between the stimuli. Note also that saccades with larger GE (i.e. around the

midpoint of the two stimuli) are more similar in latency across all conditions than saccades with smaller GE, consistent with our understanding of non-specific early visual transients followed by slower signals that are more task-modulated.

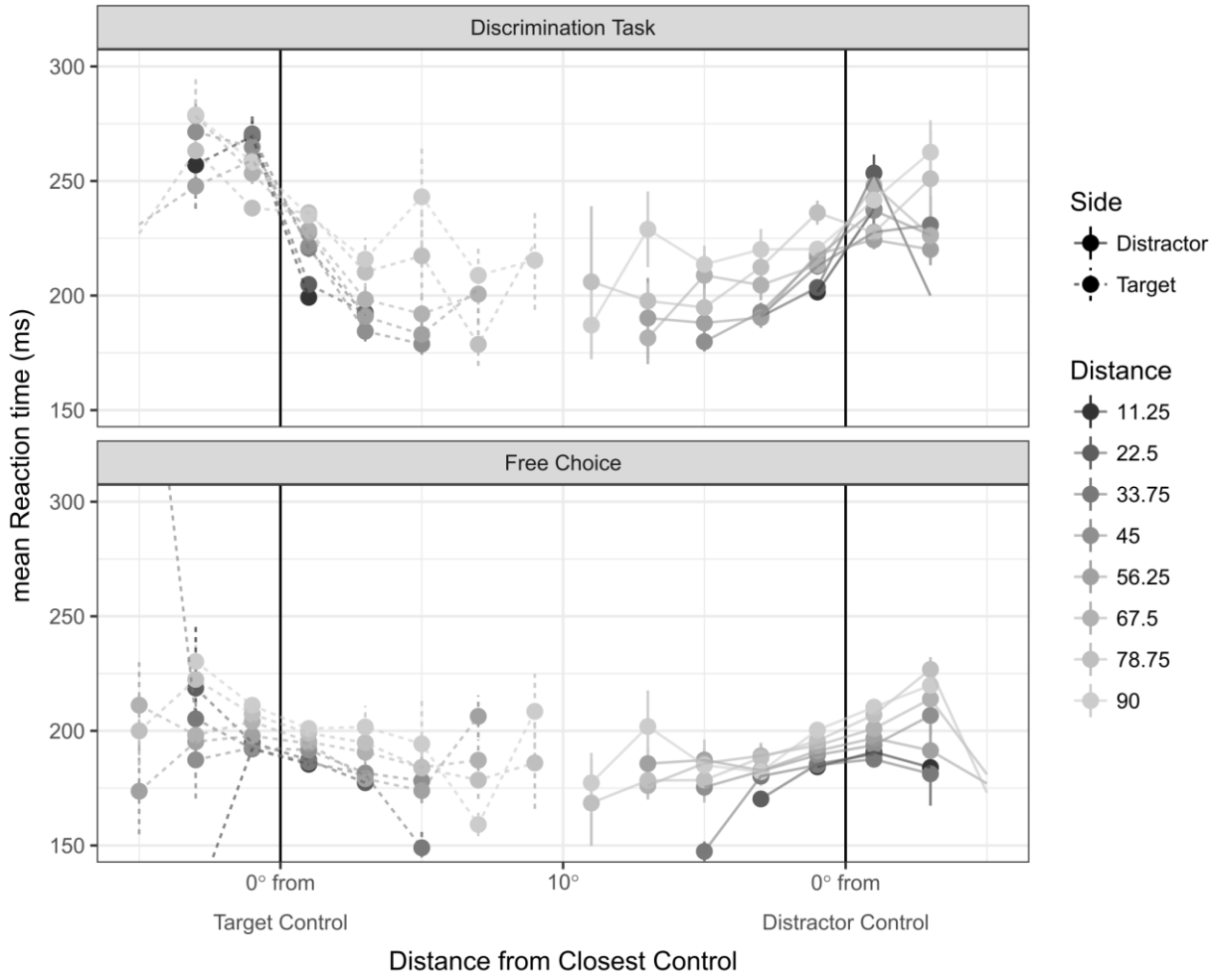


Figure 8: Reaction times in relation to the bimodal GE (or Distance from the Closest Attractor). *The mean reaction times are plotted for each 2 degree bins of the Distance from the Closest Attractor distribution. The DFCA was introduced in Figure 5 and is our measure of the bimodal GE.*

5.2 Asymmetric Effect of Task-Type on bimodal GE

Figure 9A corresponds to the effect of *Task-Type* on GE, which is the difference between the dark and light gray curves in **Figure 6**A. The U-tests revealed a significant effect on the DFCA only at one distance (45°) on the target side, but a consistently significant effect for all distances but one (56.25°) on the distractor side. Furthermore, the effect observed at 45° on the target side is a decrease in GE (shift toward the target) wherease the effect on the distractor side is a consistent increase in GE (shift toward the center) (**Figure 9**A, the exact statistical values are reported in the appendix). In particular, that increase of GE on the distractor side is rather regular over stimulus distances if we ignore the decrease at 56.25°; certainly, it does not show a monotonic decrease with distance. In summary, we observe an asymmetric increase in the GE when the participant is asked to aim towards a target and avoid a distractor (Discrimination) – the clearest effect is that the saccades directed to the distractor tend to be shifted toward the center (towards the target). That result when interpreted along with the **Figure 2** suggests that the discrimination mechanism is applying a boost on the target side and little or no inhibition on the distractor side: when the target loses the race, its activity at the moment the saccade was executed was higher in the discrimination task than in the free choice task, but when the distractor loses the race there is not much detectable difference in its activity level between tasks.

These GE modulations are not likely to be explained by the latencies. **Figure 10**A shows the effect of Task-Type on latencies, which is the difference between the dark and light gray curves in **Figure 6**B. The U-tests revealed that latencies are greater in the Discrimination task than in the Free Choice task on both stimulus sides (Target and Distractor). The effect size is slightly greater on Target side (mean HLΔ ~ 20 ms) than Distractor side (mean HLΔ ~ 13ms; Welch Two Sample $t(9.12) = -4.55$, $p = .001$). Although the GE is known to negatively correlate with latencies, that difference of 7 ms is not likely to explain the asymmetry in GE observed in **Figure 9**A. In comparison, the work of Heeman et al. (2014) suggests that a difference of ~120ms is needed to observe a total suppression of GE. Finally, **Figure 6**B, suggests an interaction effect of Frequency with Task Type on latencies (confirmed below); the effect of Discrimination (over FreeChoice) is less in F20 (compare the dashed curves) than in F80 (compared the solid curves). Such an interaction effect does not seem to be present for the GE (**Figure 6**A) and could not explain the GE modulation observed in **Figure 9**A.

5.3 SYMMETRIC EFFECT OF PAIR-FREQUENCY ON BIMODAL GE

Figure 9B shows the effect of *Pair-Frequency* on GE, which is the difference between the dashed and solid curves in **Figure 6**. The U-tests yielded significant effects of *Pair-Frequency* both on S1 side and S2 side (we are now ignoring whether they were target or distractor). In particular, **Figure 9**B suggests a symmetric increase of the GE when double-stimulus trials are rare (F-20), which tends to increase progressively with the inter-stimulus distance up to distance 45°, upon which it decreases. The only possible asymmetry is that the effect of F-20 on the S2 side tends to decrease more rapidly with the inter-stimulus distance in comparison with the S1 side. This small asymmetry could be attributed to the slight difference in luminance between stimulus S1 and S2. In summary, this pattern of results, when interpreted in light of the **Figure 3**, suggests that the effect of rarity is to generally increase stimulus-related activity on the motor map (i.e. to both stimulus sides).

Again, these GE modulations are not likely to be explained by differences in latencies. **Figure 10**B shows the effect of Frequency on latencies, which is the difference between the dashed and solid curves in **Figure 6**B. The U-tests revealed that there is no obvious latency modulation between F20 and F80 conditions, so that it cannot explain the GE modulations. This lack of effect is explained by the interaction of Frequency with Task Type on latencies that we noted above (**Figure 6**B). F20 (when compared to F80) increases the latencies in the Free Choice task (see the difference between the light gray curves) while decreasing the latencies in the Discrimination task (see the difference between the black curves). The sum of these positive and negative effects leads to a null effect.

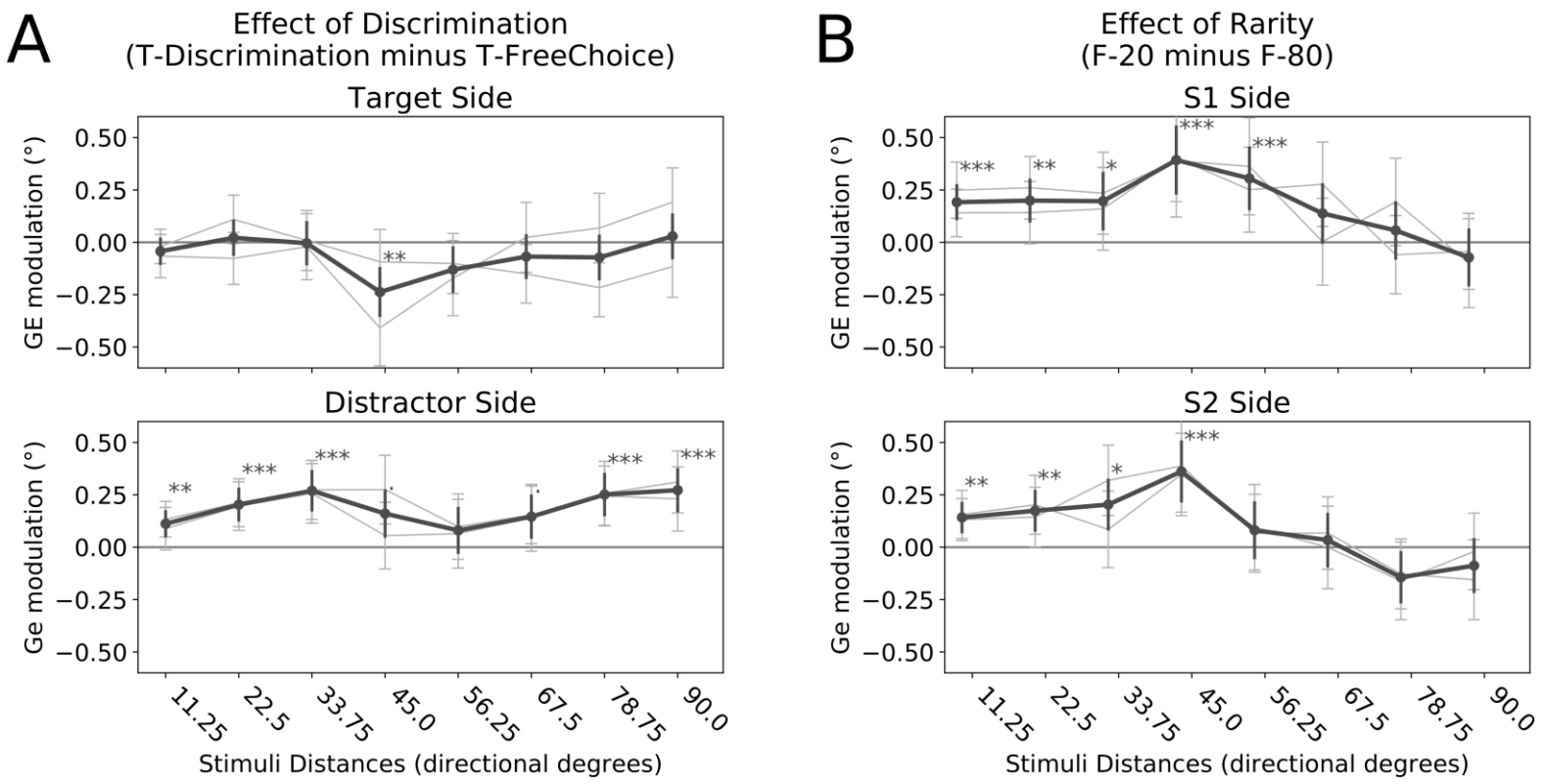
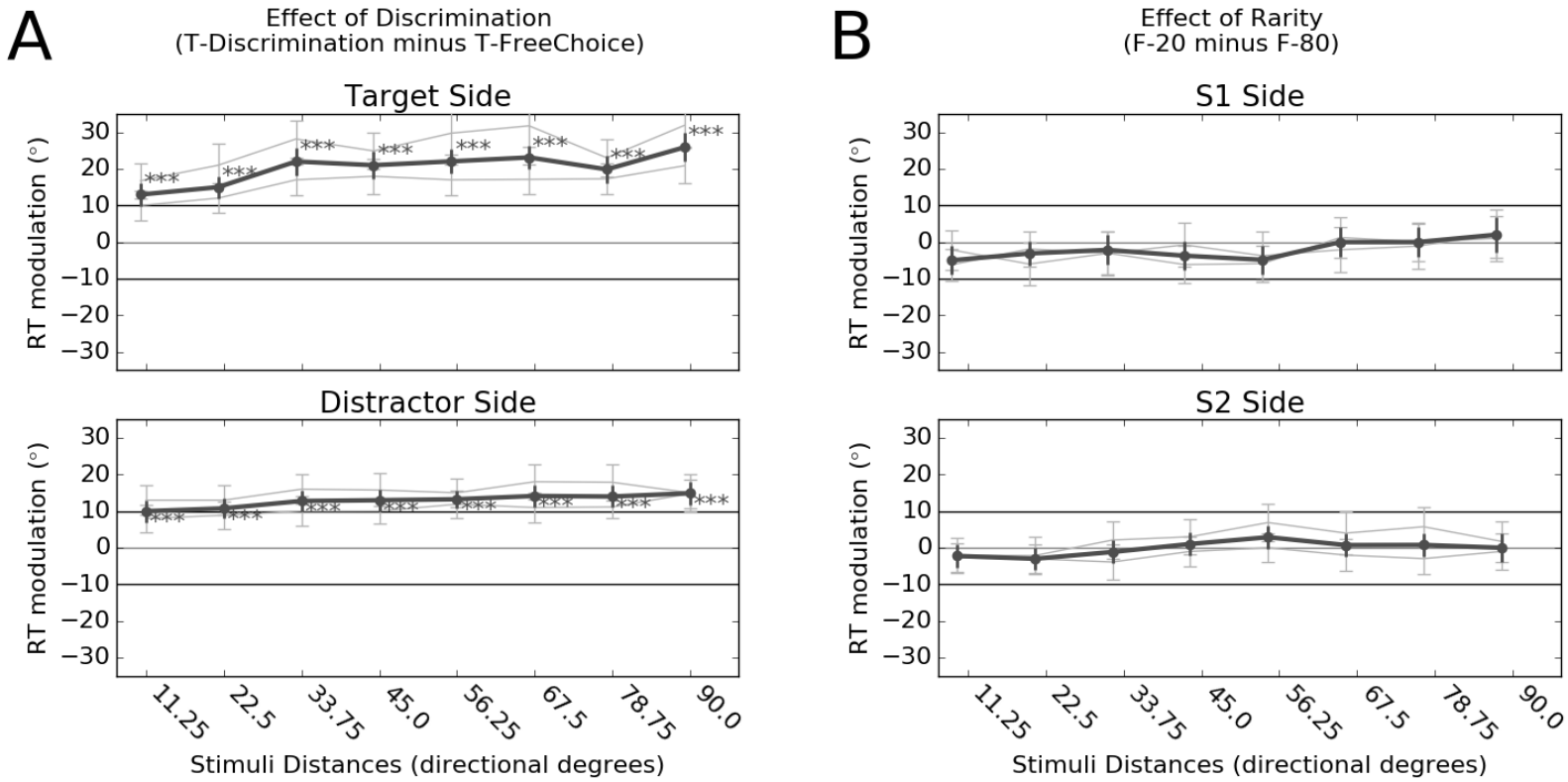


Figure 9: Summary of the Mann-Whitney U-tests on Global Effect. *Each plot shows the difference in DFCA between the two conditions, which we name the GE modulation: a positive number means that there is a larger GE (greater deviation towards the center) in Discrimination than in Free Choice conditions (in* ***subplot A****) or a larger GE in F-20 than in F-80 conditions (in* ***subplot B****). The modulation in GE – thick dark curves - is estimated with the Hodges–Lehmann estimators (HLΔ) with 95% confidence intervals. The stars represent the level of significance (*** p<.001; ** p<.01; * p<.05; . p<.1.). Finally, the thin gray curves display separately the GE modulation in the first and second block of each conditions (see method).* ***A:*** *We ignored the factor Pair-Frequency, mixing the conditions F-20 and F-80.* ***B:*** *We ignored the factor Task-Type, mixing the conditions Free Choice and Discrimination. Note that we refer to S1 and S2 as the two stimuli presented simultaneously; S2 corresponds to the slightly brighter one in Free Choice conditions and to the distractor in Discrimination conditions.*



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483 ***Figure 10: Summary of the Mann-Whitney U-tests on Latencies.*** *Each plot shows the difference in Latency between the two conditions, which we named*
484 *RT modulation. The organization is the same as in* ***Figure 9****.*

485

In order to test whether there is indeed an interaction of Frequency and Task Type on latencies, we ran a Bayesian Top-down analysis, using R's BayesFactor package (Raftery 1995; Rouder and Morey 2012), where we compared a full model (explicitly given in the caption of Table 1) to models that omit one main effect or interaction from that full. From this analysis, we can see that there is indeed an interaction effect between Task Type and Frequency on reaction times (row 4 of Table 1, BF > 1000). Note that we could not run this test on bimodal GE because its distribution varies across distances.

Table 1. Bayesian Top-down Analysis on Reaction times.

	Omitted variable	BF or 1/BF		Polarity	Interpretation T
[1]	Frequency:Side:TaskType	1.8	±4.9%	none	weak
[2]	Frequency:Side	8.1	±6.3%	against	positive
[3]	Side:TaskType	>1000	±10%	in favor	very strong
[4]	Frequency:TaskType	>1000	±92 %	in favor	very strong
[5]	Participant	>1000	±5.9%	in favor	very strong
[6]	Distance	>1000	±12%	in favor	very strong
[7]	Side	>1000	±12%	in favor	very strong
[8]	Frequency	>1000	±10%	in favor	very strong
[9]	TaskType	>1000	±11%	in favor	very strong

Note. BF stands for Bayes Factor. We inversed (1/BF) the BFs less than 1 for easier reading. We add a Polarity column that tells if the evidence quantified by the BF is against or in favor of an effect of the omitted variable (e.g. Side:TaskType). The interpretation tags give a qualitative scale to that evidence, as in Raftery (1995)*. The symbol ':' denotes an interaction. For instance, the third row reads: there is very strong evidence in favor of an interaction effect between Side and TaskType. The BFs are given against the full model:* RT ~ TaskType*Frequency*Side + Distance + Participant *with Participant as a random variable (to account for the within participant design). Side refers to the side (Target/Distractor or S1/S2) on which are the landing positions.*

5.4 INTRA-INDIVIDUAL LATENCIES AND BIMODAL GE

Finally, although we checked whether the change in mean latency across conditions could explain the change in bimodal GE, the intra-participant latency distributions could still explain part of our results. For instance, it can be argued that the lack of effect on the GE modulation on Target side (**Figure 9**) originates from a mixture of a positive GE modulation for early saccades and a negative GE modulation for late saccades. This explanation would echo the early deviation toward and late deviation away found in saccade curvature (McSorley 2006). **Figure 11** shows the same data as in **Figure 9**, except that we divided the saccade distribution into early, middle and late saccades (see the light gray, dark gray and black curves respectively). We found no consistent effect of latency groups on the bimodal GE across distances on the Target side (Figure 9A) so that the lack of target-side effect observed in Figure 7A cannot be accounted by an interaction with latencies. On the Distractor side, a more consistent pattern is observed: no effect of latencies for distances below 56.25 after which early saccades lead to small or no GE modulation while late saccades lead to large and positive GE modulation (this ordering may be present for these distances for the target side as well). We will come back to this interesting pattern in the discussion. Finally, concerning the effect of rarity, it seems that there is no obvious effect of the latency groups on the GE modulation.

Recall that we used a particular palindromic ordering for the different conditions. A Wilcoxon rank sum test on the DFCA between the first block and the second block of *F-20/Free Choice* reports a significant difference (W= 12E+7, p=0.002) with a small effect size (-0.04°) compared to the effects observed in **Figure 9** (from 0.2° to 0.4°). Thus, it appears that any extra surprise effect in the first block was small or did not last long enough within the block to produce a large overall effect. Finally, it is important to note that our results are robust despite order effects. Figure 7 shows no great change in GE modulation when taking into account either the first or the second block of each condition (thin gray curves).

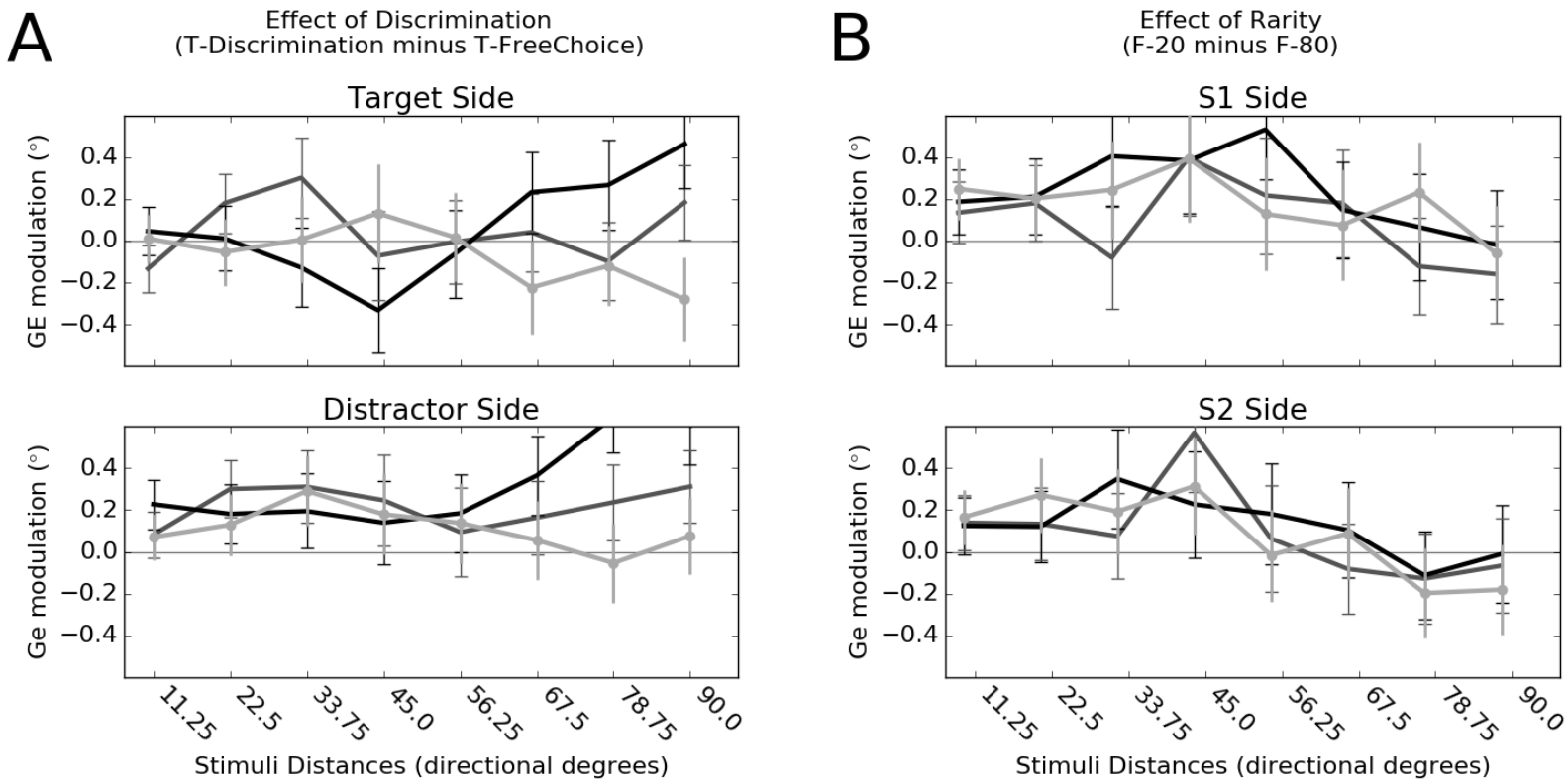

Figure 11: Effect of Latency Quantile on GE modulation. *The organization is the same as in* ***Figure 9*** *except that we split the GE modulation into three groups: early, middle, and late latency saccades, respectively in light gray, dark gray and black.*

6 DISCUSSION

In the present study, we demonstrated that, when using a pair of remote stimuli, a bimodal Global Effect (GE) occurs – i.e., both distribution modes deviated toward the other stimulus. This confirms previous reports where such an effect was shown or appeared present (Arai et al. 2004; Van der Stigchel et al. 2007, 2011). Moreover, 1) this deviation appears to occur on a nearly- straight line in visual space, and a strong curve in SC space – rather than a straight line in SC space and an outward curve (a circumference around fixation) in visual space; 2) larger deviations are associated with shorter latency. These patterns are consistent with the model architecture illustrated in Figure 1D, whereby a strong region of activity triggers a saccade while the decision process is not fully complete. Other activity remains on the map and contributes towards saccade vector programming downstream of the SC.

From this perspective, the deviation of the landing position from the race winner –that is the closest stimulus - gives an estimate of the activity of the race loser. It can then be used to assess endogenous enhancements or inhibition that the traditional GE could not distinguish. Furthermore, it can assess these signals over a wider range of interstimulus distances. We found that Task-Type and Pair-Frequency draw two clearly distinguishable patterns in terms of modulating the GE. We discuss further below the interpretation of our results, in terms of their spatial profile, underlying mechanisms, and their link with the previous literature.

6.1 EFFECT OF DISTANCE ON THE BIMODAL GLOBAL EFFECT

According to Walker et al. (1997) and Van der Stigchel and Nijboer (2013), the genuine (unimodal) GE is expected to decrease with stimulus distances. We also found this relationship in the bimodal GE (see **Figure 6**A). This may be partly explained by RT increasing with distances. However, the range of 20ms may be too small to explain the total disappearance of GE (~120ms needed in Heeman et al. 2014). In our frame of explanation, this decrease in GE with stimulus distance may also be caused either by: 1) a hypothetical stronger mutual inhibition between the two stimuli whilst their distance increases – decreasing the activity of the loser or 2) a spatially localized release of the inhibition exerted by substantia nigra pars reticulata (SNr) on the SC – remote losers would benefit less from disinhibition centered on target location (Hikosaka and Wurtz 1983; Handel and Glimcher 1999; Basso and Wurtz 2002). Note that 1) would contradict the relatively flat curve of inhibition

reported in previous modelling and neurophysiological work (Arai et al. 1994; Trappenberg et al. 2001).

6.2 Modulation of the Global Effect by Discrimination Signal

It is often assumed in discrimination tasks that top-down mechanisms facilitate the target-related activity and/or inhibit the distractor-related activity (Schall and Hanes 1993; Schall et al. 1995; Wardak et al. 2002; Ipata et al. 2006; Thomas and Paré 2007). Our work shows that the discrimination signal consistently increases the bimodal GE on the distractor side and had no consistent effect on the GE on the Target side. If we recall the predictions of **Figure 2**, which use the model described in **Figure 1**D, the increase of GE on the distractor side means that that the activity of competition loser – the target – was stronger in the Discrimination Task than in Free Choice (right-hand column in Figure 2). In other words, our results suggest that the discrimination signal is facilitating/boosting the target rather than inhibiting the distractor. This result is in line with neurophysiological data reporting more post-stimulus activity in FEF and SC on the target side during visual search (McPeek and Keller 2002; Fecteau and Munoz 2006) and no obvious inhibition on the distractor side in the SC before the saccadic burst (White et al. 2012).

However, this conclusion may seem to be in opposition with some previous work. Although it has been shown that saccade planning enhances processing at target location (Kowler et al. 1995; Deubel 2008), it was also shown that saccade execution suppresses processing at non-target locations (Khan et al. 2015). Similarly, the Basal Ganglia appear to enhance target location and inhibit distractor locations (Van Schouwenburg et al. 2013). Finally, it was suggested that local inhibition of the distractor location could explain saccadic curvature away from a distractor (Tipper et al. 2001; McSorley et al. 2004). Thus, it seems that further implementation of our paradigm could explore whether the appearance of inhibition on the distractor can be systematically controlled.

The effect of discrimination did not decrease with stimulus distances. This suggests that its mechanism is not interacting directly with the GE mechanism itself – which does decline with distance. If that decline is caused by mutual inhibition or the SNr's influence on the SC (hypothesis 1) and 2) discussed above), then the goal-directed boost seems simply additive with those mechanisms. It is known that the FEF is involved in target discrimination (Schall and Hanes 1993) and has direct projections to the brainstem saccade burst generator (although their functional role has been questioned, Hanes and Wurtz 2001), bypassing the SC to control saccades (Schiller et al. 1980;

Schiller and Sandell 1983; Schiller and Chou 1998). In the eventuality that the boost to the target is provided by the FEF, it follows that at least part of this enhancing effect is not altered by the mutual inhibition and/or the SNr's action in the SC.

6.3 Modulation of the Global Effect by Frequency

Previous studies have shown that the probability of a stimulus appearing at a *specific location* can influence the GE (He and Kowler 1989). Location probability is thought to increase the strength of the preparatory signal in the SC (Basso and Wurtz 1998; Dorris and Munoz 1998), possibly from the FEF (Liu et al. 2011), and therefore to decrease the reaction time. Our work goes further and suggests that probability of occurrence, which, unlike location probabilities, has no spatial dimension, can also influence the GE. According to our results, the rarity of occurrence of a pair of stimuli increases the bimodal GE symmetrically, as predicted in Figure 3, and this effect could not be explained by a change in reaction times. Thus, probability of occurrence tends to enhance the activity related to rare stimuli configurations and has the opposite effect of the location probability, which enhances the activity of common locations.

It can also be observed that the effect of rarity on GE decreases with stimulus distance, just as the GE itself decreases with stimulus distance. In other words, rarity is modulating – rather than being additive with – the underlying GE itself. There are at least two possible ways this could occur: 1) an increase of the responsiveness of the neurons on the motor map; 2) a decrease of lateral inhibition on the motor map. The former would modify the gain function of the neurons (i.e. increasing function, typically sigmoid, linking input current to firing rate) – varying its x offset (gating) and/or slope.

Interestingly, the norepinephrine system has been suggested to modify the gain function of neurons in diffuse parts of the brain involved in decision making through coarse projections (Hurley et al. 2004; Aston-Jones and Cohen 2005). Several studies have suggested that the norepinephrine system responds to the relevance, novelty, and rarity of stimuli (Alexinsky et al. 1990; Privitera et al. 2010; Preuschoff et al. 2011) with more or less habituation effect (Aston-Jones et al. 1994; Vankov et al. 1995). Direct projections of the Locus Coeruleus to the SC have been found (Edwards et al. 1979; Mooney et al. 1990; Arce et al. 1994) while high and stable concentration of norepinephrine decreased the spontaneous and/or stimulus-evoked responses in SC (Mooney et al. 1990; Tan et al. 1999; Zhang et al. 1999). Taken together, these findings would encourage investigations into whether the norepinephrine system could be the mechanism behind the effect of rarity on the strength of the

GE. If this is indeed the case, it would open a new avenue of experimental work to test the effect of the norepinephrine on decision making.

Regarding the latencies for our rarity manipulation, we believe there are three interacting factors acting in different directions: the rarity boost discussed above; caution; spatial probability. In **Figure 6**B, in the Discrimination Task condition, the reaction times are smaller in F20 than in F80 while in the Free Choice condition, reaction times are smaller in F80 than in F20. Concerning the Discrimination task, an explanation is that frequent discrimination trials (i.e. F80) raises caution, which leads to slower reaction times. In that case, rare discrimination trials (see black dashed curve) would lead to lower caution and to similar reaction times as rare free choice (gray dashed curve) – which is what we observe. Concerning the Free Choice condition, we can consider the opposite effect of spatial probability: in F80, there is a rate of 1.8 stimuli per trial appearing on the 13.5° eccentricity ring, while in F20, this rate drops to 1.2. The higher rate leads to a higher spatial probability, which leads to faster reaction time in F80 as we observed. To conclude, our results suggest that once other factors are brought into play, what increases the bimodal GE does not necessarily decrease the reaction times, and vice-versa.

In the literature, it has been shown that high probability of occurrence of the target in a go/no-go paradigm increases the proportion of express saccade (Jüttner and Wolf 1992) while the high probability of a distractor being present seems to decrease the reaction time on trials in which it is indeed present (Goldstein and Beck 2013). However, these paradigms may not be testing the same mechanisms as ours. In Jüttner and Wolf (1992), the saccadic system likely learns to inhibit the go-signal when the go-trials are rare while our paradigm only has go-trials. In Goldstein and Beck (2013), it is possible that, because the distractor is informative of the future target timing and position, it acts as a warning cue.

6.4 CONCLUSION:

The present work has generated a novel way to assess decision processes and signals occurring in an action selection map such as the SC. In particular, we have examined a different aspect of the Global Effect which we have termed the bimodal Global Effect (GE). Unlike the traditionally defined Global Effect (Walker et al. 1997), the bimodal GE can be observed for distant stimuli and for bimodal distributions. We see it as a tool to measure the modulations that occur on the side of the stimulus that loses the race to trigger a saccade. Using this framework allowed us to assess in more depth the

effect of frequency of choice and of active discrimination on the action selection map. We believe that this framework opens a new avenue to explore decision making in general.

7 APPENDICES

[The following tables are given for the reviewers, but they may not be included in the final version. They can be found on the open science framework webpage.]

7.1 TABLES

The condition effects (difference between conditions) are reported with the Hodges–Lehmann estimator (HLΔ). It is the median of all possible differences between the N measures in one condition and the M measures in another condition (N x M combinations).

A non-parametric 0.95 confidence interval for HLΔ accompanies these estimates. Finally, the Common Language Effect Size (CLES) (McGraw and Wong 1992; Vargha and Delaney 2000) from the R package `orddom` is reported. Indeed, the CLES simply estimates the probability that a DFCA randomly picked from one distribution is higher than a DFCA randomly picked from another distribution – also known as the Probability of Superiority. Generally speaking, a CLES of 0% (or 100%) would mean that the first distribution is lower (or higher) and does not overlap with the second distribution. When the CLES is at 50% the medians of both distributions are aligned.

Table 1: Target Side U-tests over distances for a distractor type effect (Free Choice against Discrimination):

Distance	U-stat		p-value	n.Td	n.Ts	CLES	HLΔ	95% CI	
11.25	433851		1.00E+00	981	915	51.67%	-0.040	-0.102	0.022
22.5	460714		1.00E+00	997	909	49.16%	0.028	-0.059	0.115
33.75	458158		1.00E+00	983	930	49.88%	0.005	-0.101	0.110
45	412946	**	2.78E-03	998	914	54.73%	-0.219	-0.338	-0.099
56.25	432647		2.55E-01	1063	863	52.84%	-0.119	-0.230	-0.011
67.5	479230		1.00E+00	1065	925	51.35%	-0.056	-0.161	0.049
78.75	430544		1.00E+00	1035	858	51.52%	-0.062	-0.168	0.045
90	451448		1.00E+00	1007	881	49.11%	0.037	-0.070	0.143

Note. Refer to Table 2 note.

Table 2: Distractor Side, U-tests over distances for a distractor type effect (Free Choice against Discrimination):

Distance	U-stat		p-value	n.F8	n.F2	CLES	HLΔ	95% CI	
11.25	452304	**	5.10E-03	970	1023	54.42%	-0.118	-0.185	-0.050

22.5	423556	***	5.45E-06	950	1024	56.46%	-0.205	-0.285	-0.125
33.75	413434	***	3.81E-07	948	1017	57.12%	-0.275	-0.373	-0.177
45	451307	*	3.88E-02	953	1022	53.66%	-0.166	-0.282	-0.051
56.25	442758		8.91E-01	877	1054	52.10%	-0.091	-0.204	0.021
67.5	397084	*	3.35E-02	869	990	53.84%	-0.157	-0.266	-0.050
78.75	415780	***	7.91E-06	904	1055	56.40%	-0.265	-0.372	-0.159
90	406350	***	2.51E-06	915	1026	56.72%	-0.284	-0.394	-0.176

Note. Refer to Table 2 note.

Table 3: Target Side, U-tests over distances for a distractor frequency effect (F-20 against F-80):

Distance	**U-stat**		**p-value**	**n.F8**	**n.F2**	**CLES**	**HLΔ**	**95% CI**	
11.25	225235	***	2.52E-05	1550	346	58.00%	-0.192	-0.273	-0.111
22.5	259148	**	1.35E-03	1516	390	56.17%	-0.202	-0.309	-0.097
33.75	252640	.	5.10E-02	1555	358	54.62%	-0.193	-0.332	-0.055
45	228095	***	3.26E-05	1566	346	57.90%	-0.384	-0.549	-0.219
56.25	245242	***	7.39E-04	1565	361	56.59%	-0.297	-0.449	-0.148
67.5	279013		6.15E-01	1625	365	52.96%	-0.126	-0.268	0.014
78.75	267306		1.00E+00	1536	357	51.25%	-0.051	-0.186	0.085
90	287083		1.00E+00	1525	363	48.14%	0.074	-0.059	0.207

Note. Refer to Table 2 note.

Table 4: Distractor Side, U-tests over distances for a distractor frequency effect (F-20 against F-80):

Distance	**U-stat**		**p-value**	**n.F8**	**n.F2**	**CLES**	**HLΔ**	**95% CI**	
11.25	376754	**	4.34E-03	1556	437	44.59%	0.142	0.062	0.222
22.5	344744	**	4.80E-03	1582	392	44.41%	0.176	0.076	0.275
33.75	360737	*	1.44E-02	1538	427	45.07%	0.198	0.074	0.320
45	387352	***	1.15E-05	1537	438	42.46%	0.356	0.210	0.503
56.25	323915		1.00E+00	1517	414	48.42%	0.069	-0.069	0.208
67.5	299833		1.00E+00	1451	408	49.35%	0.027	-0.105	0.158
78.75	302211		1.29E-01	1532	427	53.80%	-0.154	-0.281	-0.028
90	295816		1.00E+00	1540	401	52.10%	-0.090	-0.226	0.047

Note. Refer to Table 2 note.

8 REFERENCES

Alexinsky T, **Aston-Jones G**, **Rajkowski J**, **Revay RS**. Physiological correlates of adaptive behavior in a visual discrimination task in monkeys. In: *Society for Neuroscience Abstracts*. 1990, p. b1.

Arai K, **Keller EL**. A model of the saccade-generating system that accounts for trajectory variations produced by competing visual stimuli. *Biol Cybern* 92: 21–37, 2004.

Arai K, **Keller EL**, **Edelman JA**. Two-dimensional neural network model of the primate saccadic system. *Neural Netw* 7: 1115–1135, 1994.

Arai K, **McPeek RM**, **Keller EL**. Properties of Saccadic Responses in Monkey When Multiple Competing Visual Stimuli Are Present. *J Neurophysiol* 91: 890–900, 2004.

Arce EA, **Bennett-Clarke CA**, **Rhoades RW**. Ultrastructural organization of the noradrenergic innervation of the superficial gray layer of the hamster's superior colliculus. *Synapse* 18: 46–54, 1994.

Aston-Jones G, **Cohen JD**. An integrative theory of locus coeruleus-norepinephrine function: adaptive gain and optimal performance. *Annu Rev Neurosci* 28: 403–450, 2005.

Aston-Jones G, **Rajkowski J**, **Kubiak P**, **Alexinsky T**. Locus coeruleus neurons in monkey are selectively activated by attended cues in a vigilance task. *J Neurosci* 14: 4467–4480, 1994.

Awh E, **Belopolsky AV**, **Theeuwes J**. Top-down versus bottom-up attentional control: a failed theoretical dichotomy. *Trends Cogn Sci* 16: 437–443, 2012.

Basso MA, **Wurtz RH**. Modulation of Neuronal Activity in Superior Colliculus by Changes in Target Probability. *J Neurosci* 18: 7519–7534, 1998.

Basso MA, **Wurtz RH**. Neuronal Activity in Substantia Nigra Pars Reticulata during Target Selection. *J Neurosci* 22: 1883–1894, 2002.

Blakesley RE, **Mazumdar S**, **Dew MA**, **Houck PR**, **Tang G**, **Reynolds CF**, **Butters MA**. Comparisons of Methods for Multiple Hypothesis Testing in Neuropsychological Research. *Neuropsychology* 23: 255–264, 2009.

Boehnke SE, **Munoz DP**. On the importance of the transient visual response in the superior colliculus. *Curr Opin Neurobiol* 18: 544–551, 2008.

Bompas A, **Sumner P**. Saccadic Inhibition Reveals the Timing of Automatic and Voluntary Signals in the Human Brain. *J Neurosci* 31: 12501–12512, 2011.

Bompas A, **Sumner P**. Saccadic inhibition and the remote distractor effect: One mechanism or two? *J Vis* 15: 15–15, 2015.

Casteau S, **Vitu F**. On the effect of remote and proximal distractors on saccadic behavior: A challenge to neural-field models. *J Vis* 12, 2012.

Cousineau D. Confidence intervals in within-subject designs: A simpler solution to Loftus and Masson's method. *Tutor Quant Methods Psychol* 1: 42–45, 2005.

Deubel H. The time course of presaccadic attention shifts. *Psychol Res* 72: 630, 2008.

Deubel H, **Wolf W**, **Hauske G**. The evaluation of the oculomotor error signal. *Adv Psychol* 22: 55–62, 1984.

Dorris MC, **Munoz DP**. Saccadic Probability Influences Motor Preparation Signals and Time to Saccadic Initiation. *J Neurosci* 18: 7015–7026, 1998.

Edwards SB, **Ginsburgh CL**, **Henkel CK**, **Stein BE**. Sources of subcortical projections to the superior colliculus in the cat. *J Comp Neurol* 184: 309–329, 1979.

Fecteau JH, **Munoz DP**. Salience, relevance, and firing: a priority map for target selection. *Trends Cogn Sci* 10: 382–390, 2006.

Findlay JM. Global visual processing for saccadic eye movements. *Vision Res* 22: 1033–1045, 1982.

Findlay JM, **Walker R**. A model of saccade generation based on parallel processing and competitive inhibition. *Behav Brain Sci* 22: 661–674, 1999.

Gandhi NJ, **Katnani HA**. Motor Functions of the Superior Colliculus. *Annu Rev Neurosci* 34: 205–231, 2011.

Goldstein RR, **Beck MR**. The Effect of Distractor Presentation Frequency on Saccade Reaction Times & Curvature. *trials* 24: 001, 2013.

Goossens HHLM, **Van Opstal AJ**. Dynamic Ensemble Coding of Saccades in the Monkey Superior Colliculus. *J Neurophysiol* 95: 2326–2341, 2005.

Goossens HHLM, **Van Opstal AJ**. Dynamic Ensemble Coding of Saccades in the Monkey Superior Colliculus. *J Neurophysiol* 95: 2326–2341, 2006.

Goossens HHLM, **Van Opstal AJ**. Optimal control of saccades by spatial-temporal activity patterns in the monkey superior colliculus. *Plos Comput Biol* 8: e1002508–e1002508, 2012.

Handel A, **Glimcher PW**. Quantitative Analysis of Substantia Nigra Pars Reticulata Activity During a Visually Guided Saccade Task. *J Neurophysiol* 82: 3458–3475, 1999.

Hanes DP, **Wurtz RH**. Interaction of the Frontal Eye Field and Superior Colliculus for Saccade Generation. *J Neurophysiol* 85: 804–815, 2001.

He P, **Kowler E**. The role of location probability in the programming of saccades: Implications for ā€ center-of-gravityā€\= tendencies. *Vision Res* 29: 1165–1181, 1989.

Heeman J, **Theeuwes J**, **Van der Stigchel S**. The time course of top-down control on saccade averaging. *Vision Res* 100: 29–37, 2014.

Hikosaka O, **Wurtz RH**. Visual and oculomotor functions of monkey substantia nigra pars reticulata. IV. Relation of substantia nigra to superior colliculus. *J Neurophysiol* 49: 1285–1301, 1983.

Hurley L, **Devilbiss D**, **Waterhouse B**. A matter of focus: monoaminergic modulation of stimulus coding in mammalian sensory networks. *Curr Opin Neurobiol* 14: 488–495, 2004.

Ipata AE, **Gee AL**, **Goldberg ME**, **Bisley JW**. Activity in the Lateral Intraparietal Area Predicts the Goal and Latency of Saccades in a Free-Viewing Visual Search Task. *J Neurosci* 26: 3656–3661, 2006.

Jüttner M, **Wolf W**. Occurrence of human express saccades depends on stimulus uncertainty and stimulus sequence. *Exp Brain Res* 89: 678–681, 1992.

Katnani HA, **Gandhi NJ**. Order of operations for decoding superior colliculus activity for saccade generation. *J Neurophysiol* 106: 1250–1259, 2011.

Katnani HA, **Van Opstal AJ**, **Gandhi NJ**. A test of spatial temporal decoding mechanisms in the superior colliculus. *J Neurophysiol* 107: 2442–2452, 2012.

Khan AZ, **Blohm G**, **Pisella L**, **Munoz DP**. Saccade execution suppresses discrimination at distractor locations rather than enhancing the saccade goal location. *Eur J Neurosci* 41: 1624–1634, 2015.

Kopecz K. Saccadic reaction times in gap/overlap paradigms: a model based on integration of intentional and visual information on neural, dynamic fields. *Vision Res* 35: 2911–2925, 1995.

Kopecz K, **Schöner G**. Saccadic motor planning by integrating visual information and pre-information on neural dynamic fields. *Biol Cybern* 73: 49–60, 1995.

Kowler E, **Anderson E**, **Dosher B**, **Blaser E**. The role of attention in the programming of saccades. *Vision Res* 35: 1897–1916, 1995.

Lee C, **Rohrer WH**, **Sparks DL**. Population coding of saccadic eye movements by neurons in the superior colliculus. *Nature* 332: 357–360, 1988.

Liu C-L, **Tseng P**, **Chiau H-Y**, **Liang W-K**, **Hung DL**, **Tzeng OJL**, **Muggleton NG**, **Juan C-H**. The Location Probability Effects of Saccade Reaction Times Are Modulated in the Frontal Eye Fields but Not in the Supplementary Eye Field. *Cereb Cortex* 21: 1416–1425, 2011.

Marino RA, **Trappenberg TP**, **Dorris M**, **Munoz DP**. Spatial interactions in the superior colliculus predict saccade behavior in a neural field model. *J Cogn Neurosci* 24: 315–336, 2012.

McGraw KO, **Wong SP**. A common language effect size statistic. *Psychol Bull* 111: 361, 1992.

McKinney W. Data structures for statistical computing in Python [Online]. In: *Proceedings of the 9th Python in Science Conference*, p. 51–56. http://204.236.236.243/proceedings/scipy2010/pdfs/mckinney.pdf [22 May 2015].

McPeek RM. Incomplete Suppression of Distractor-Related Activity in the Frontal Eye Field Results in Curved Saccades. *J Neurophysiol* 96: 2699–2711, 2006.

McPeek RM, **Han JH**, **Keller EL**. Competition Between Saccade Goals in the Superior Colliculus Produces Saccade Curvature. *J Neurophysiol* 89: 2577–2590, 2003.

McPeek RM, **Keller EL**. Saccade Target Selection in the Superior Colliculus During a Visual Search Task. *J Neurophysiol* 88: 2019–2034, 2002.

McSorley E. Time Course of Oculomotor Inhibition Revealed by Saccade Trajectory Modulation. *J Neurophysiol* 96: 1420–1424, 2006.

McSorley E, **Haggard P**, **Walker R**. Distractor modulation of saccade trajectories: spatial separation and symmetry effects. *Exp Brain Res* 155: 320–333, 2004.

Mooney RD, **Bennett-Clarke C**, **Chiaia NL**, **Sahibzada N**, **Rhoades RW**. Organization and actions of the noradrenergic input to the hamster's superior colliculus. *J Comp Neurol* 292: 214–230, 1990.

Nyström M, **Hooge I**, **Holmqvist K**. Post-saccadic oscillations in eye movement data recorded with pupil-based eye trackers reflect motion of the pupil inside the iris. *Vision Res* 92: 59–66, 2013.

Ottes FP, **Van Gisbergen JA**, **Eggermont JJ**. Latency dependence of colour-based target vs nontarget discrimination by the saccadic system. *Vision Res* 25: 849–862, 1985.

Ottes FP, **Van Gisbergen JA**, **Eggermont JJ**. Visuomotor fields of the superior colliculus: a quantitative model. *Vision Res* 26: 857–873, 1986.

Perez F, **Granger BE**. IPython: A System for Interactive Scientific Computing. *Comput Sci Eng* 9: 21–29, 2007.

Phongphanphanee P, **Marino RA**, **Kaneda K**, **Yanagawa Y**, **Munoz DP.**, **Isa T**. Distinct local circuit properties of the superficial and intermediate layers of the rodent superior colliculus. *Eur J Neurosci* 40: 2329–2343, 2014.

Preuschoff K, **'t Hart BM**, **Einhauser W**. Pupil Dilation Signals Surprise: Evidence for Noradrenaline's Role in Decision Making. *Front Neurosci* 5, 2011.

Privitera CM, **Renninger LW**, **Carney T**, **Klein S**, **Aguilar M**. Pupil dilation during visual target detection. *J Vis* 10: 3, 2010.

Raftery AE. Bayesian model selection in social research. *Sociol Methodol* 25: 111–164, 1995.

Robinson DA. Eye movements evoked by collicular stimulation in the alert monkey. *Vision Res* 12: 1795–1808, 1972.

Rouder JN, **Morey RD**. Default Bayes factors for model selection in regression. *Multivar Behav Res* 47: 877–903, 2012.

Sailer U, **Eggert T**, **Ditterich J**, **Straube A**. Global effect of a nearby distractor on targeting eye and hand movements. *J Exp Psychol Hum Percept Perform* 28: 1432, 2002.

Satel J, **Fard FS**, **Wang Z**, **Trappenberg TP**, **others**. Simulating oculomotor inhibition of return with a two-dimensional dynamic neural field model of the superior colliculus [Online]. *Aust J Intell Inf Process Syst* 14, 2014.

https://www.researchgate.net/profile/Jason_Satel/publication/267990591_Simulating_oculomotor_inhibition_of_return_with_a_two-dimensional_dynamic_neural_field_model_of_the_superior_colliculus/links/550624b80cf24cee3a051f00.pdf [16 Feb. 2016].

Satel J, **Wang Z**, **Trappenberg TP**, **Klein RM**. Modeling inhibition of return as short-term depression of early sensory input to the superior colliculus. *Vision Res* 51: 987–996, 2011.

Schall JD, **Hanes DP**. Neural basis of saccade target selection in frontal eye field during visual search. *Nature* 366: 467–469, 1993.

Schall JD, **Hanes DP**, **Thompson KG**, **King DJ**. Saccade target selection in frontal eye field of macaque. I. Visual and premovement activation. *J Neurosci* 15: 6905–6918, 1995.

Schall JD, **Purcell BA**, **Heitz RP**, **Logan GD**, **Palmeri TJ**. Neural mechanisms of saccade target selection: gated accumulator model of the visual-motor cascade: Gated accumulator for visuomotor cascade. *Eur J Neurosci* 33: 1991–2002, 2011.

Schiller PH, **Chou IH**. The effects of frontal eye field and dorsomedial frontal cortex lesions on visually guided eye movements. *Nat Neurosci* 1: 248–253, 1998.

Schiller PH, **Sandell JH**. Interactions between visually and electrically elicited saccades before and after superior colliculus and frontal eye field ablations in the rhesus monkey. *Exp Brain Res* 49: 381–392, 1983.

Schiller PH, **True SD**, **Conway JL**. Deficits in eye movements following frontal eye-field and superior colliculus ablations. *J Neurophysiol* 44: 1175–1189, 1980.

Tan H, **Mooney RD**, **Rhoades RW**. Effects of norepinephrine upon superficial layer neurons in the superior colliculus of the hamster: in vitro studies. *Vis Neurosci* 16: 557–570, 1999.

Tandonnet C, **Massendari D**, **Vitu F**. When larger visual distractors become less disruptive: Behavioral evidence for lateral inhibition in saccade generation. *J Vis* 12: 2, 2012.

Tandonnet C, **Vitu F**. Stimulus properties and saccade metrics: When local features are more critical than global features. *Behav Neurosci* 127: 121, 2013.

Thomas NWD, **Paré M**. Temporal Processing of Saccade Targets in Parietal Cortex Area LIP During Visual Search. *J Neurophysiol* 97: 942–947, 2007.

Tipper SP, **Howard LA**, **Jackson SR**. Selective reaching to grasp: Evidence for distractor interference effects. *Vis Cogn* 4: 1–38, 1997.

Tipper SP, **Howard LA**, **Paul MA**. Reaching affects saccade trajectories. *Exp Brain Res* 136: 241–249, 2001.

Trappenberg TP, **Dorris MC**, **Munoz DP**, **Klein RM**. A model of saccade initiation based on the competitive integration of exogenous and endogenous signals in the superior colliculus. *J Cogn Neurosci* 13: 256–271, 2001.

Van der Stigchel S, **Meeter M**, **Theeuwes J**. The spatial coding of the inhibition evoked by distractors. *Vision Res* 47: 210–218, 2007.

Van der Stigchel S, **Nijboer TC**, **Bultitude JH**, **Rafal RD**. Delayed oculomotor inhibition in patients with lesions to the human frontal oculomotor cortex: Evidence from a study on saccade averaging. *Brain Cogn* 82: 192–200, 2013.

Van der Stigchel S, **Nijboer TCW**. How global is the global effect? The spatial characteristics of saccade averaging. *Vision Res* 84: 6–15, 2013.

Van der Stigchel S, **Vries JP**, **Bethlehem R**, **Theeuwes J**. A global effect of capture saccades. *Exp Brain Res* 210: 57–65, 2011.

Van Opstal AJ, **Goossens HHLM**. Linear ensemble-coding in midbrain superior colliculus specifies the saccade kinematics. *Biol Cybern* 98: 561–577, 2008.

Van Schouwenburg MR, **Den Ouden HEM**, **Cools R**. Selective Attentional Enhancement and Inhibition of Fronto-Posterior Connectivity by the Basal Ganglia During Attention Switching. *Cereb. Cortex* (December 15, 2013). doi: 10.1093/cercor/bht345.

Vankov A, **Hervé-Minvielle A**, **Sara SJ**. Response to Novelty and its Rapid Habituation in Locus Coeruleus Neurons of the Freely Exploring Rat. *Eur J Neurosci* 7: 1180–1187, 1995.

Vargha A, **Delaney HD**. A critique and improvement of the CL common language effect size statistics of McGraw and Wong. *J Educ Behav Stat* 25: 101–132, 2000.

Walker R, **Deubel H**, **Schneider WX**, **Findlay JM**. Effect of remote distractors on saccade programming: evidence for an extended fixation zone. *J Neurophysiol* 78: 1108–1119, 1997.

Walton MMG, **Sparks DL**, **Gandhi NJ**. Simulations of Saccade Curvature by Models That Place Superior Colliculus Upstream From the Local Feedback Loop. *J Neurophysiol* 93: 2354–2358, 2005.

Wang Z, **Kruijne W**, **Theeuwes J**. Lateral interactions in the superior colliculus produce saccade deviation in a neural field model. *Vision Res* 62: 66–74, 2012a.

Wang Z, **Satel J**, **Hilchey MD**, **Klein RM**. Averaging saccades are repelled by prior uninformative cues at both short and long intervals. *Vis Cogn* 20: 825–847, 2012b.

Wang Z, **Satel J**, **Trappenberg TP**, **Klein RM**. Aftereffects of saccades explored in a dynamic neural field model of the superior colliculus. *J Eye Mov Res* 4: 1–16, 2011.

Wardak C, **Olivier E**, **Duhamel J-R**. Saccadic Target Selection Deficits after Lateral Intraparietal Area Inactivation in Monkeys. *J Neurosci* 22: 9877–9884, 2002.

White BJ, **Munoz DP**. The superior colliculus. *Lateral* 3: 4, 2011.

White BJ, **Theeuwes J**, **Munoz DP**. Interaction between visual-and goal-related neuronal signals on the trajectories of saccadic eye movements. *J Cogn Neurosci* 24: 707–717, 2012.

Wilimzig C, **Schneider S**, **Schöner G**. The time course of saccadic decision making: Dynamic field theory. *Neural Netw* 19: 1059–1074, 2006.

892 **Zhang Y**, **Mooney RD**, **Rhoades RW**. Effects of norepinephrine on the activity of visual neurons in
893 the superior colliculus of the hamster. *Vis Neurosci* 16: 541–555, 1999.

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